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ARTICLE II.

THE MAMMALIA OF THE DEEP RIVER BEDS.

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Read before the American Philosophical Society, October 6, 1893.

The ninth Princeton geological expedition to the Tertiary formations of the Far West selected as its field of operations the valley of Smith river, or Deep creek, as it is variously called, in central Montana. The party, which was under the direction of the writer and Prof. W. F. Magie, consisted of the following students: Messrs. Butler, Benet, Coulter, Hosford, Jefferson and Stevenson, and spent a part of the summer of 1891 in exploring the very limited outcrops of lacustrine beds in the region mentioned. We had the good fortune to secure the services of Prof. O. C. Mortson, of Great Falls, Mont., as a guide, and to his minute knowledge of the country and zealous labors the success of the undertaking is in large measure due.

Many gentlemen in Great Falls, White Sulphur Springs and Livingston took great interest in the work of the expedition and rendered every assistance in their power. To enumerate all of those to whom we are under obligations for many kindnesses would be impossible, but special thanks are due to the Hon. Paris Gibson and Mr. W. W. Connor, of Great Falls, but for whose most kind and prompt assistance at a critical period the trip would necessarily have been abandoned.

GEOLOGICAL MUSEUM, PRINCETON, N. J., September 20, 1893.

The literature of the Deep River or "*Ticholeptus*" beds is rather limited, as the region has been comparatively little explored. The formation was first discovered by Grinnell and Dana, in 1875, and their brief account may be quoted almost in full.

"During the explorations carried on last summer under the direction of Col. William Ludlow, Corps of Engineers, a series of Tertiary deposits were identified by the writers near Camp Baker, Montana. These deposits indicate the existence in

this region of a Miocene lake basin, which was succeeded by another lake basin in Pliocene time.

“Camp Baker [the spot marked Logan on the map herewith given] is situated on Deep creek, a stream which flows into the Missouri river above Sun river. It lies about fifty miles due east of Helena. It is surrounded on all sides by mountains, of which the Big Belt range, lying immediately to the south or southwest, is the highest and most conspicuous. . . .

“The Tertiary beds found here consist, for the most part, of homogeneous cream-colored clays, so hard as to be with difficulty cut with a knife. The beds are horizontal and rest unconformably upon the upturned red and yellow slates below. The clays of which they are formed resemble closely those found in the Miocene [*i. e.*, White River] beds at Scott's Bluffs, near the North Platte river, in Wyoming. The deposits at Camp Baker have been extensively denuded and nowhere reach any great thickness. At a point about three miles southeast of the Post, some bluffs were noticed where the Miocene beds attained a thickness of about two hundred feet, and these were capped by fifty feet of the Pliocene clays, both beds containing characteristic fossils. In the underlying Miocene beds were found a species of *Rhinoceros*, several species of *Oreodon* Leidy and *Eporeodon* Marsh, a canine tooth apparently of *Elotharium* Pomel and remains of Turtles. In the Pliocene beds the principal fossils were a species apparently of *Merychys* Leidy, remains of an equine smaller than the modern horse, and Pliocene Turtles. These fossils have not yet been carefully studied, and for this reason their relations to the remains found in the other lake basins of similar age cannot be stated.

“We saw the first exposures of these beds a few miles west of the Sulphur Springs. . . . This point is about six miles southeast of Camp Baker. From here, the bed was traced continuously along Deep creek for a distance of fifteen miles, extending quite up to the mountains, on the eastern side at least. Beds of the same character, containing similar fossils, were found on White-Tailed Deer creek, a branch of Deep creek, about seven miles to the north of Camp Baker, as well as on Camas creek, to the southwest of the Post. Traces of this deposit, containing what appear to be remains of *Rhinoceros*, were also found two miles or more south of Moss Agate Springs and at a considerable elevation above the creek bed. With more time than we had at command, they could no doubt have been traced much farther, although in many places the beds have been washed out or have been covered by the later local drift.

“These Tertiary beds were all laid down after the elevation of the mountains and the igneous eruptions. They are, as has been said, perfectly horizontal, and are

often seen covering over ridges of trachyte. The line of separation between the Miocene and Pliocene beds is in some places well marked. It consists of about six feet of hard sands, interstratified with layers of very small water-worn pebbles soldered together into a hard mass, but very easily picked out with a knife. Immediately above the strata of pebbles the Pliocene fossils were found. In several places fragments of trachyte were noticed in the Pliocene beds" (No. 18, pp. 126-128).

The next account of this formation was given by Cope, who had sent his assistant, Isaacs, to collect in the valley and described a number of new forms from it. His collection embraced specimens from the upper beds only, those called Pliocene by Grinnell and Dana, and these he referred to the Loup Fork. In 1879 (No. 3), Cope divided the Loup Fork into two horizons, which he called the *Ticholeptus* and *Procamelus* beds respectively, the former being the beds of the Deep River region. Subsequently (Nos. 6, 8, 10), Cope raised the *Ticholeptus* beds to a rank coördinate with that of the John Day or the Loup Fork, and gives the following list of species as occurring in the Montana area: *Mastodon proavus*, *Protohippus sejunctus*, *Merycochærus montanus*, *Merychys zygomaticus*, *M. pariogonus*, *Cyclopidius simus*, *C. emylinus*, *Pithecistes brevifacies*, *P. decedens*, *P. heterodon*, *Procamelus* vel *Protolabis* sp. *Blastomeryx borealis* (No. 8, p. 369). In his latest paper on the subject, this writer defines the formation as follows: "TICHOLEPTUS. *Mammalia*. Presence of *Anchitherium*, Proboscidea and Camelidæ and the Oreodont genera *Merycochærus*, *Merychys*, *Cyclopidius* and *Pithecistes*. Absence of ? *Elotheriidae*, ? *Poebrotheriidae*, ? *Nimravidæ* and *Cosoryx*. This horizon requires further exploration, as but twenty species have been thus far determined from it. But it is evidently intermediate in age between the John Day and Loup Fork epochs, with greater affinities to the latter. It differs from the latter in the presence of *Anchitherium*, numerous genera and species of *Oreodontidae*, and in the absence of *Cosoryx*. The formation is known from three regions: first, from western Nebraska; second, from the valley of Deep river, Montana; and third, from Cottonwood creek, Oregon. Its thickness has not yet been stated" (No. 6, pp. 456, 457).

It should be noted that in these lists the name *Anchitherium* is used for the John Day equines, to which, in this paper, I have applied Marsh's name, *Miohippus*, for reasons which will appear later. This point is of importance.

In 1891, I published a brief note upon the subject of this horizon (No. 31). At that time the fossils collected were still in the matrix, and only the hasty examinations in the field were available for the purposes of comparison. Consequently, a number of errors crept into the work, so as to greatly vitiate its conclusions, which will not be further referred to here. In a second note (*American Naturalist*, 1893,

p. 660) I gave preliminary definitions of the new genera and species contained in the collections made by the Princeton party.

Now that this collection has been worked over and can be compared with Prof. Cope's material from the same locality, some definite statements may be made with regard to the geological and palæontological relations of the Deep River beds. So far as the stratigraphy is concerned, there is little to add to the account of Grinnell and Dana, except in one particular. The statements of these authors seem to imply that the two sets of beds are conformable throughout, but there is strong evidence which goes to show that this is not the case. In the first place, there is a marked lithological contrast between the two series, the lower being very hard and the upper, for the most part, incoherent sands, though nodules of harder material have, in many cases, formed around the bones. The general character of the lower beds is very much like that of the older Miocene, the White River or John Day, while the upper are more like the Loup Fork. Though both sets of strata are generally horizontal, with local exceptions, the upper beds appear to rest upon an eroded surface of the underlying strata. Thus, at one point, the older beds, as exposed in a line of buttes—apparently, at least—rise higher than an exposure of the newer strata across the ravine from the first exposure. In the absence of instruments, this point could not be determined quite certainly, but it is very probable. Towards the north and east the upper beds appear to extend beyond the lower and to produce an unconformity by overlap. Finally, the fossil contents of the two series of strata are very strikingly different, not a single species of mammal and not more than two genera are common to the two, and those genera range from the John Day into the upper Loup Fork. Such radical and sudden changes are hardly to be explained on the hypothesis of migration, and point to a considerable hiatus between the times of deposition of the two sets of strata.

The following species of mammals were found in the lower beds: *Cynodesmus thooides* Scott, *Steneofiber montanus* Scott, *Cænopus* sp., *Miohippus annectens?* Marsh, *M. anceps?* Marsh, *M. (Anchitherium) equiceps?* Cope, *Mesoreodon chelonyx* Scott, *M. intermedius* Scott, *Poebrotherium* sp., *Hypertragulus calcaratus* Cope. This list appears to be a scanty one, but this is explained by the fact that the exposures which yielded well-preserved fossils are very limited in extent, a few acres at most, and when we compare them with the vast regions over which collections from the other Tertiary formations have been gathered, the disproportion will not seem so striking. Indeed, I know of very few spots of equal extent which have yielded so large a number of individuals and species. The facies of this fauna is undeniably that of the John Day Miocene. All of the genera but two, and several of the species, occur

in the typical Oregon localities, and while, owing to the very small area of the Montana beds, we cannot lay much stress upon the absence of certain characteristic John Day forms, yet the presence of such relatively modernized genera as *Cynodesmus* and *Mesoreodon* indicates that these beds should be referred to the summit of the John Day formation. This is of interest as being the first identification of this horizon east of the Rocky mountains.

The upper beds, which Grinnell and Dana called Pliocene, present a very different assemblage of species. Cope's collection, so far as I can judge, was gathered entirely from these beds and contains nothing from the lower horizon. His collection and that made by the Princeton party are, as would naturally be expected, not quite coëxtensive, each containing some forms which the other does not. Combining the two, we obtain the following list: *Canis? anceps* Scott, *Chalicotherium? sp.*, *Aphelops sp.*, *Miohippus sp.*, *Anchitherium equinum* Scott, *Desmatippus crenidens* Scott, *Protohippus sejunctus* Cope, *Protohippus (Merychippus) insignis* Leidy, *Merychys (Ticholeptus) zygomaticus* Cope, *M. pariogonus* Cope, *Merycochærus montanus* Cope, *Cyclopidius simus* Cope, *C. emydinus* Cope, *C. incisivus* Scott, *Pitheciastes brevifacies* Cope, *P. decedens* Cope, *P. heterodon* Cope, *Protolabis sp.*, *Procamelus sp.*, *Blastomeryx borealis* Cope, *B. antelopinus* Scott, *Mastodon proavus* Cope. In addition to this list should be mentioned a considerable number of equine animals, which cannot be well identified, as the specimens are scattered vertebræ, limb and foot bones, not accompanied by teeth, but which, from the variations in size and details of construction, point to several species not enumerated above.

The resemblance of this fauna to that of the Loup Fork has been obvious from the first, for it was doubtless the latter formation to which Grinnell and Dana referred under the name "Pliocene." For the same reason of very limited exposures, as in the case of the lower beds, when compared with the John Day of Oregon, we cannot insist very strongly upon the absence of typical Loup Fork genera from the upper series of Deep River strata. Of much greater significance is the occurrence in the latter of five genera and fourteen species of mammals which have not been found in the vastly more extensive and carefully examined Loup Fork deposits. This fact, having regard to the character of the species involved, points to the conclusion, already drawn by Cope, that these beds are older than the typical Loup Fork horizon, but their faunal connection with that horizon is so close that there seems little ground for considering the Deep River as an "epoch" of coördinate rank with the three other Miocene epochs. The relation between the Deep River and Loup Fork beds is more intimate than that between the Wind River and the Bridger proper of the Eocene. My own preference is, therefore, to refer both series to the Loup Fork,

as Cope originally did, and then subdivide that formation into two horizons. The names which Cope first proposed for these subdivisions, the *Ticholeptus* and *Procamelus* beds respectively, are inapplicable, for the former name is a synonym of *Merychius*, a genus which occurs in both horizons, and, as now appears, *Procamelus* probably does also.

I cannot agree with Cope in regarding the strata of western Nebraska and Cottonwood creek, Oregon, as referable to the same horizon as those of the Deep river valley, in Montana. In the case of the former, the determination rests chiefly upon the presence there of *Leptauchenia*, which Hayden found associated with *Oreodon*, *Ischyromys*, *Hyracodon* and other characteristic White River forms (see Leidy, No. 23, pp. 20, 21). Cope has questioned the correctness of this statement as to *Leptauchenia*, but it has been abundantly confirmed, that genus being an undoubted White River form. Hayden's reference of *Merycochoerus* and *Protomeryx* to this same horizon is almost certainly erroneous and has not been confirmed by subsequent observers. The reference of the beds developed along Cottonwood creek and the upper John Day river, in Oregon, to the Deep River horizon, is determined by the occurrence in them of a so-called *Anchitherium* and of a species identified as *Blastomeryx borealis*. It should be noted, however, that the term *Anchitherium* is used in the sense of *Miohippus*, the species from Montana which I have called *A. equinum* is a very different animal and belongs to the group of *A. aurelianense*, of Europe, which it equals in size. *Miohippus* is found in the typical Loup Fork, as well as in the lower series (see Osborn, No. 28, p. 89, under the title ?*Anchitherium parvulum*). No great weight, therefore, can be attached to the occurrence of the genus in the Cottonwood Creek beds. The presence of *Blastomeryx borealis* would, of itself, be insufficient for the correlation of the two localities, but the identification of the species is not at all certain. Besides certain minor differences in the teeth, the limb bones from the Oregon beds indicate the existence there of two species, both of which are much heavier than the Montana forms and more like others from the Loup Fork of Kansas. Cope, himself, was struck by the faunal differences of the two localities. He says: "The only species common to the two lists is the *Blastomeryx borealis*, a fact which indicates some important differences in the two horizons, either epochal or faunal" (No. 8, p. 369).

Present evidence appears, therefore, to point to the conclusion that the upper series of strata developed in the valley of Deep river form a well-marked horizon at the base of the Loup Fork, and that they are not exactly paralleled by any deposits as yet known elsewhere; and, further, that the lower series of the Montana strata should be referred to the summit of the John Day, where they form a less distinctly

marked horizon. Together, the two series tend to bridge over the gap between the John Day, on the one hand, and the typical Loup Fork, though they by no means completely close the hiatus. It is a more difficult task to correlate these beds with their European equivalents. The Loup Fork horizon was referred by Leidy and Hayden to the Pliocene, a view which is still maintained by some authorities, but, as Cope has shown, the determination rests upon the supposed occurrence in these beds of forms having a very modern facies, and which were very probably derived from newer overlying strata, since, in typical Loup Fork exposures not covered by these newer beds, the modernized forms have not been found. The recent discovery of the Blanco beds, of Texas, with their true Pliocene fauna (see Cope, No. 11), lends additional force to Cope's contention that the Loup Fork should be referred to the upper Miocene. Branco has objected to this correlation, as follows:

“Eine scharfe Parallelisirung wird hier durch die verschiedene Zusammensetzung der beiderseitigen Faunen erschwert. Auf der einen Seite fehlen der Loup Fork Gruppe echt miocaene Formen wie *Anthracotherium* und *Anchitherium* und es treten dafür Geschlechter von jugendlicherem Aussehen wie *Protohippus* und *Hippidium* auf. Andererseits aber repräsentiren nicht nur die amerikanischen *Oreodontidae* ungefähr ein mit dem europäischen *Cenotherium* übereinstimmendes Entwicklungsstadium, sondern beiden Faunen sind auch direct *Steneofiber*, *Amphicyon*, *Tetralophodon*, *Hipparion* und *Procervulus* gemeinsam. Man wird also mit Cope diese Parallelisirung der Loup-Fork-Gruppe mit dem Miocæn Europa's im Allgemeinen gelten lassen müssen, wenn gleich man nicht übersehen darf, dass dieselbe durch Formen wie *Protohippus* und *Hippidium*, welche dem Pferde der Jetztzeit bereits recht nahe stehen, sowie durch das Vorkommen von *Dicotyles*, *Hystrix* und *Mustela* einen entschiedenen jugendlicheren Charakter erhält als die miocaene Fauna Europa's” (No. 2, p. 149).

These objections rest, for the most part, upon the incorrect identifications of European and American genera, which were current at the time Branco's paper was written. As will be seen in the sequel, *Anchitherium* is present in the lower Loup Fork and not in the White River and John Day, the equines of which formations have been erroneously referred to that genus. The absence of *Anthracotherium* from the Loup Fork is of no weight, since the genus is quite unknown in America. The occurrence of *Hystrix*, *Dicotyles* and *Mustela* in the Loup Fork beds is extremely doubtful, the identifications being made on very imperfect specimens. The reference of *Hippidium* to this horizon is also very doubtful and has not been confirmed. If, as is almost certainly the case, the equine series is of American origin, there is nothing surprising in the fact that the series should be, on this continent, one stage in

advance of its contemporaries in Europe, just as the American ruminants in several horizons lag behind their contemporaries of the Old World. Further, to regard the Loup Fork as Pliocene involves the assertion that *Procamelus* in America was contemporary with *Camelus* in Asia, which, seeing that the camel series is of American origin, is most improbable.

Of the European faunas, that of Sansan and Simorre offers the best analogy with that of the Deep River beds. In both continents this horizon is marked by the first appearance of the mastodons, and, since the Proboscidea would seem to have originated in neither Europe nor America, but to have reached both regions by migration, this fact is significant. *Anchitherium*, in the restricted sense in which I have used that word, is likewise common to both, and, as this genus has a very restricted range in time, it is a most important fossil. *Blastomeryx* is exceedingly like the Sansan species of *Palæomeryx*, though more primitive in some respects. No stress can be laid upon the supposed *Amphicyon* and *Procervulus* of the Loup Fork, as these names are incorrectly given to the American forms.

If Dall's contention, that North and South America were not united until the close of the Miocene (No. 12, p. 21), be confirmed, the Loup Fork will necessarily be referred to the Pliocene, as is indicated by the occurrence in those beds of the glyptodont genus, *Caryoderma* Cope, a South American type, though the genus itself has not yet been obtained in that continent. But the evidence for the date of the elevation of Central America and the Isthmus of Panama is by no means conclusive. Gabb's statement is to the effect that "The communication between the Atlantic and Pacific in the region of Costa Rica was interrupted in the Pliocene *or subsequent to the deposition of the mass of the Miocene strata*" (italics mine) (quoted in Dall and Harris, No. 12, p. 188, from Gabb's MS. report). This is quite compatible with the view that the connection of the two continents was made before the end of the Miocene. If we may provisionally regard the Deep River beds (upper series) as equivalent to those of Sansan and Steinheim, the John Day would consequently be about equivalent to the lower Miocene of St. Gérard le Puy, though probably somewhat older, and the White River to the beds of Rouzon or the "Marnes lacustres." The term Oligocene has not been found necessary in this country, the line between the Uinta and White River beds being a clear and convenient demarcation between the Eocene and Miocene. Nevertheless, much confusion and incorrect reasoning have resulted from calling the White River simply Miocene. The presence of such genera as *Hyænodon*, *Hemipsalodon*, *Mesonyx*, *Elotherium*, *Hyopotamus*, etc., sufficiently proves these beds to be more ancient than the true Miocene of Europe,

and it would be much to the advantage of clearness and consistency if the White River were called Oligocene, a view for which Cope has long contended.

In the descriptive portion of this paper the fossils will be treated according to their systematic position, as the interest attaching to them is especially morphological. The lack of smaller animals in the collections is very noticeable. The lower beds have yielded but one rodent and the upper none at all; only two carnivores, both dogs, have been found. None of the Insectivora or Chiroptera have been detected. The fauna, as so far known, consists, therefore, almost entirely of medium and large-sized ungulates, for which the conditions of fossilization are, no doubt, chiefly responsible.

CARNIVORA.

Canidæ.

CYNODESMUS Scott.

(Pl. I, Figs. 1-5.)

Amer. Naturalist, 1893, p. 660.

Canine animals having the dentition of the microdont forms of *Canis*, but with the skull structure of the ancient genera. Cerebral hemispheres small, not overlapping the olfactory lobes or cerebellum, and with fewer and simpler convolutions than any of the recent *Canidæ*. Postglenoid foramen concealed or absent.

CYNODESMUS THOÖIDES Scott.

(*loc. cit.*)

Dentition microdont; deuterocone of upper sectorial relatively well developed; face short, cranium elongate; small frontal sinuses present; mandible non-lobate with stout angular hook and broad, recurved coronoid; size medium.

The technical distinction of this genus from *Cynodictis* is by no means easy, and yet it becomes very clear on an examination of the two; while the latter very probably represents a side branch, leading away from the direct canine phylum, the former may, with equal probability, be regarded as being either in the direct line of canine descent or but little removed from it.

In order to make clear the character of this interesting form, it will be most convenient to compare it carefully with some typical modern species, for which purpose the coyote, *Canis latrans*, will be taken as a standard.

I. DENTITION. A. *Upper Jaw*. The incisors are very small and form a nearly straight row, the external pair projecting but little behind the others. The first and

second are of nearly equal size, while the third is somewhat larger, though the difference is much less marked than in *C. latrans* or even than in the John Day species, *Temnocyon coryphæus*; the teeth are crowded together, not spaced apart as in the latter species. The diastema between the external incisor and the canine is rather short. The latter is as well developed, relatively, as in the coyote, but of a somewhat different form, being more oval and less compressed in section; the depression on the inner face and its anterior bounding ridge of enamel are also less marked.

Except for their relative shortness (antero-posteriorly) and height, the premolars closely resemble those of the modern species. P.1 is a very small and simple tooth, implanted by a single fang; the crown is of compressed conical shape, without posterior cingulum. P.2 is much larger, though small as compared with the same tooth in *C. latrans*; it is of elongated, compressed, conical form, but has no posterior basal cusp (tritocone) such as occurs in the coyote. P.3 is a still larger tooth of similar construction, except that a small tritocone and posterior cingulum have been added, which, however, are less conspicuous than in *C. latrans*. The sectorial (p 4) differs but little in any respect from that of the existing microdont species of *Canis*; the protocone exceeds the tritocone less in antero-posterior extent than in the coyote, and the deutocone is much more distinctly developed than in that species, so that the transverse diameter of the crown is greater, not only in proportion to the antero-posterior diameter (length) and to the size of the whole skull, but actually as well. In some recent species of *Canis*, however, the deutocone is quite as well developed. The premolars are quite closely crowded together and set obliquely to the line of the alveolus, so as to slightly overlap one another; posteriorly, the two lines of premolars diverge quite rapidly, while the molars converge, so that the angulation between the two series is very marked.

The first molar is wider proportionately to its fore and aft length than in *C. latrans*, and the external cusps, para- and metacones are lower, more conical, and less angulate and pyramidal in shape than in the coyote. The cingulum is very strongly developed at the antero-external angle of the crown, so as almost to deserve the name of a parastyle, while it becomes very faintly marked upon the metacone. The inner elements of the crown, the protocone and crescentic cingulum, are not nearly so prominent as in the coyote; the anterior conule is slightly better developed, and the posterior distinctly less so, than in that animal. M.2 is much reduced; the external cingulum is faintly marked, except on the paracone, and the internal one not nearly so strongly developed as in *Canis latrans*.

B. Lower Jaw. The incisors are very small and set closely together, and, as is usual in the dogs, the second pair are crowded back out of line with the others; in

dimensions, they increase regularly from the first to the third. The median pair are too much worn to show whether they possessed bifid crowns, but this is clearly the case in the second and lateral pair; the posterior groove which indicates this structure is more median in position than in the modern form. The canines are shaped very much as in the latter, but are shorter and diverge less towards their apices.

The first premolar resembles the corresponding upper tooth, having a very small and simple crown supported on a single root. The succeeding premolars increase regularly in size up to the fourth; essentially they are all alike—compressed, trenchant, acute and quite high cones; on $\overline{p.3}$, and more distinctly on $\overline{p.4}$, a posterior basal cusp and cingulum appear, but they are less developed than in *C. latrans*.

The first, or sectorial molar, is characteristically cynoid, but retains some primitive features. Compared with the inferior sectorial of the coyote, the following differences are apparent: (1) The protoconid is relatively higher, less compressed, and more conical in shape, shorter in the fore and aft dimension, and its anterior border is much more steeply inclined and nearly vertical; (2) the paraconid is lower and less extended antero-posteriorly; (3) the talon is lower, and, while it is as broad as the anterior portion of the crown (trigonid), and therefore entirely different from that of *Temnocyon*, yet its basin-like character is less emphasized than that of *Canis*, owing to the smaller size and less elevation of the entoconid; the metaconid corresponds in size and position to that of *Canis*. The differences enumerated are slight and yet not without importance; for whenever the sectorial of *Cynodesmus* departs in structure from that of *Canis*, it is in the direction of *Daphænus* and the creodonts. $\overline{M.2}$ differs in no tangible respect from that of the coyote. $\overline{M.3}$ is not so much reduced as in that species and has a more elongate oval crown, which is supported on two fangs, while, in the recent representatives of the family, the fang is very generally single.

II. THE SKULL. The skull preserves many of the primitive characters which occur in the ancient genera, such as *Temnocyon* and *Daphænus*. This is particularly marked in the long, narrow cranium, with postorbital constriction placed far back of the orbits, and the short face, which is due partly to the microdont dentition and the anterior position of the orbits, they being farther forward than in *Canis*. The basi-cranial axis, as measured by Huxley's method (No. 19, p. 239), is strikingly long, actually exceeding that of the considerably larger skull of *C. latrans*. This elongation of the cranium does not, however, imply a correspondingly long cerebral fossa, as may be seen from the position of the postorbital constriction, which marks the anterior boundary of the hemispheres, and which, in this genus, is much farther removed from the orbits than in the recent members of the family, in which it follows

close behind the orbits. The cerebral fossa is not only narrow, therefore, but it is short, extending only slightly above the cerebellar fossa, and the lengthening of the basicranial axis more particularly affects the floor of the latter. In the fossil which is under description, the roof of the brain-case and the occiput, together with the condyles, have been weathered away, and therefore the conformation of the sagittal and occipital crests cannot be determined with certainty; but, from the character of the frontal ridges and the shape of the cranial cast, which is well preserved, there can be little doubt that these crests were very much as in *Temnocyon coryphæus*, to the skull of which species that of *Cynodesmus* bears a very close resemblance.

The upper contour of the skull is nearly straight and the descent at the forehead very slight and gradual, in which respect we find a great similarity in shape to the fox's skull. The basioccipital (so much of it as is preserved) is narrower than in *Canis*, broader and more flattened than in *Temnocyon*; in the latter, this bone is anteriorly much narrowed by the extremely large bullæ, and posteriorly displays a median longitudinal convexity, with a deep fossa on each side of it. In the species before us, the paroccipital process is very different from that of *Canis*; in the latter it is "long and prominent, and its anterior surface is applied closely to the back part of the bulla, but to a less extent than in the cats, as the process is more compressed. The mastoid is distinct but slightly developed" (Flower, No. 14, p. 24). In *Cynodesmus*, as in *Temnocyon*, the paroccipital process is much longer, more compressed, and more curved downward and backward; its free portion is much more widely separated from the bulla, with which the process is connected by a narrow bridge of bone, which expands anteriorly so that the contact surface between the two is about as in the existing genus. The mastoid is somewhat more exposed on the surface of the cranium than in *Canis* and is more lateral in position, the paroccipital processes occupying the inferior angles of the occiput. This displaces the mastoid processes anteriorly, so that, as in *Temnocyon*, they are on the sides of the skull and overlapped by the squamosal; they are somewhat more developed than in *Canis*. The tympanics are inflated into large auditory bullæ, which equal in actual size, and therefore proportionally exceed, those of *Canis latrans*, though they are much less prominent than in *Temnocyon coryphæus*. So far as can be judged from the specimen, the bulla appears to be divided by a septum, in very much the same manner as in *Canis*, into two widely communicating chambers, of which the postero-internal is much the larger. The meatus auditorius is an irregularly oval opening, which does not form a tube; the anterior lip is, however, extended outward more than in *Canis* and, separated only by a narrow slit from the postglenoid process of the squamosal, articulates with it at its extremity. The shape and development of the bulla produce

some differences in the disposition of the foramina in its neighborhood; thus, the foramen lacerum posterius extends less around the hinder end of the bulla and is confined to its postero-internal angle, running almost parallel to the basicranial axis. Still more important is the fact that the anterior lip of the auditory meatus, extending along the postglenoid process, overlaps and conceals the glenoid foramen. Indeed, I cannot altogether satisfy myself that the foramen is present at all; but there is a long, narrow and curved slit between the lip and the process, which probably contains the entrance to the foramen. In *Temnocyon coryphæus* the foramen occupies the position of the slit just mentioned, but is much more conspicuous, resembling the same structure in the raccoon.

The zygomatic arches are relatively longer and more massive than in *Canis*; they arch outward as far, but much less strongly upward, and thus, when seen from the side, pursue a straighter course. The root of the zygomatic process of the squamosal is continued backward as a broad shelf over the mastoid process, as is also the case in *Temnocyon coryphæus* though not in *Canis*. The glenoid cavity is more extended transversely than in the latter, and is more concave, the hinder margin being elevated into a ridge, which rises gradually into the postglenoid process, which is longer and more curved anteriorly than in the coyote. The jugal is very long and extends backward to the outer angle of the glenoid cavity; the masseter ridge is more prominent and rugose, and the masseter surface wider than in the recent animal; the postorbital angle, which is but slightly developed in the latter, does not appear at all. The anterior end of the jugal is bifurcate and the inferior branch descends lower upon the molar alveolus than in the coyote. The lachrymal has about the same extent upon the face as in that species, but possesses a spine in the form of an obtuse ridge; the foramen is single and placed entirely within the orbit.

The specimen does not permit us to determine the share taken by the frontals in forming the roof of the cranium, but they possess considerable extension upon the face. The supraciliary ridges are well marked and rugose and converge rapidly to form the sagittal crest; clearly, no lyrate "sagittal area" could have been present. The forehead is not so flattened as in *Temnocyon*, but slightly arched from side to side, and the postorbital processes are hardly more developed than in that form and consequently much less so than in *Canis latrans*. The nasal processes are very long and nearly reach the premaxillaries, though in this respect there is some asymmetry in the specimen, the process on the left side being appreciably longer than that on the right. Small frontal sinuses are present. The nasals are relatively long, and are broader and more convex from side to side than in the coyote; the anterior border is not emarginate, but obliquely truncate and considerably longer than in the recent

animal. The anterior nares are higher, more oval in shape and more inclined backward than in *Temnocyon coryphæus*, less so than in *Canis latrans*. In the former they are small, nearly circular in shape and vertical in position. The horizontal portion of the premaxillæ is shorter, less massive and rounded than in the coyote, in correlation with the smaller incisors, and at the symphysis the two are less closely applied. The ascending portion is also quite differently shaped; it is much longer, broader and more steeply inclined, and its superior and anterior borders pass into each other almost imperceptibly, while in the coyote the two meet at an angle not very much greater than a right angle. The palatal portion differs but little from that seen in the latter species, but the incisive foramina are somewhat more anterior in position and encroach less upon the maxillaries.

The maxillary, in its extension upon the face, is short, but relatively deep vertically, and this height rapidly increases backward, so that the premaxillary suture is steeply inclined. The canine alveoli cause more marked prominences upon the face than in *Canis latrans*, and the muzzle is more constricted behind them. The infra-orbital foramen is nearer to the orbit than in that species, but occupies the same position with reference to the teeth, opening above the interval between p. 3 and p. 4. The palatal processes are somewhat narrower than in the coyote, and the suture between them is marked by a low rugose ridge. The palatines have a less extent, both in length and breadth, than in the modern form, their anterior borders, which in the latter reach to the interval between p. 3 and p. 4, hardly extending beyond the middle of the sectorial. On the other hand, the front margin of the posterior nares is quite behind the molar alveoli, while in the coyote it is opposite the front of m. 2; the palatal notches are also much less deeply marked than in the latter. The posterior nares are long and narrow and somewhat constricted in the middle of their course; the pterygoids have larger hamular processes than in the coyote and the pterygoid fossæ are better marked.

The mandible differs in important respects from that of *Canis latrans*. The horizontal ramus is shorter, but deeper and thicker; the chin rises more steeply, which produces less procumbency in the incisors; the lower border is more sinuously curved, descending more abruptly from beneath the coronoid, and the angular hook longer and stouter. The ascending ramus has a greater antero-posterior extent, and the coronoid is broader, more inclined backward, and with more curved posterior margin; its anterior border is wider and more distinctly defined and displays a groove for the attachment of the buccinator and maxillo-labial muscles, which would seem to indicate that these muscles were better developed than in the existing form. This broad anterior surface is reflected over upon the upper border, where it forms a

very distinctly marked, flattened and obliquely inclined surface for the insertion of the temporal muscle; its upper margin, however, is a thin edge, not thickened and rugose as in the coyote; its lower margin forms the upper boundary of the masseteric fossa and is continuous with the prominent ridge which bounds that depression anteriorly. The nearest approximation to this character of the coronoid which I have been able to find among the recent *Canidæ* occurs in *C. cinereo-argentatus*. The masseteric fossa is large and profound, indicating a powerful muscle, which is further confirmed by the character of the surface on the jugal for the origin of the masseter. The condyle is somewhat flattened upon its postero-superior aspect; it is much more extended transversely than in *Canis latrans*, and this extension is most marked in the portion external to the coronoid.

The cranial foramina, with the exception of the foramen lacerum posterius and the glenoid foramen, which have already been noticed, depart in no respect from those of *Canis*. The mandible has a large mental foramen beneath $\overline{p.2}$ and a smaller one under $\overline{p.3}$, which are closer together than in the coyote; the dental foramen occupies the same position as in that species.

III. *The Brain.* The cranial cast displays characters very different from those of the recent *Canidæ*, both in its general proportions and in the details of the cerebral convolutions. The hemispheres are narrow in proportion to their length and taper gradually forward; their contour is rather more alopecoid than thooid, according to Huxley's distinctions. "In the Fox the contour of the brain, viewed from above, is that of a pear with the narrow end forwards, laterally the contour is undulated, presenting one slight incurvation in the region of the sylvian sulcus and another in that of the supraorbital [*i. e.*, presylvian] sulcus, while a little angulation marks the junction of the olfactory lobes with the cerebral hemispheres. In *Canis azaræ* the cerebral hemispheres immediately behind the supraorbital fissure widen out abruptly and the lateral contour, instead of being slightly incurved at this point, presents a sharp rectangular inflection. The frontal lobe anterior to the supraorbital sulcus is much longer in *C. azaræ* than in *C. vulpes* and the brain is considerably wider behind in the latter" (No. 19, pp. 245-247). In *Cynodesmus*, the posterior widening of the alopecoid brain does not occur, but the anterior portion is more like what occurs in those animals than in the thooids, though simpler than in either. The hemispheres slightly overlap the lateral lobes of the cerebellum, but are notched in the middle, so as to leave the vermis free. Owing to the relatively well-developed tempero-sphenoidal lobes, the cerebrum has considerable vertical depth in this region, but anteriorly it is very shallow as well as narrow. Apparently, the hemispheres leave the olfactory lobes quite exposed. Except for its greater width pos-

teriorly, the brain of the fennec (*Canis zerda*) has a very similar outline to that of the fossil.

We can best examine the sulci of the hemispheres after quoting Krueg's description of the fissures which are characteristic of the recent *Canidæ*: "Fissura anterior und postica sind immer vorhanden, fast immer verbunden. Fissura coronalis, ansata, lateralis, medilateralis meistens verbunden, letztere sowie die ectolateralis immer vorhanden. Die Fissura splenialis ist häufig mit der rhinalis posterior, nur ausnahmsweise nicht mit der cruciata verbunden. Die Fissura prorea, præcruciata, posteruciata und confinis fehlen häufig und sind auch bei den grösseren Species nie stark entwickelt" (No. 21, p. 614). In *Cynodesmus* the cerebral convolutions are much simpler than in any existing species of *Canidæ*, even the smallest. Besides the sylvian fissure, the dorsal aspect of the hemispheres displays but two slightly curved sulci, one of which, the superior, is clearly the lateral sulcus; its anterior portion may, perhaps, represent the ansate and coronal fissures, but if so, all three are in the same straight line. In the recent species the three are usually connected, but with the difference that the ansate and coronal sulci are curved downwards and forwards, out of the line taken by the lateral. The second fissure in the specimen is the suprasylvian, which is remarkably short and little curved, and is not continued into the posterior suprasylvian, which appears to be absent. The crucial fissure is not indicated on the cast, but no great stress can be laid upon this fact, for this sulcus is sometimes not shown in the intracranial casts of recent species, the brains of which actually possess it. If present, however, in *Cynodesmus*, it must have been extremely short, as is shown by the straight course of the lateral sulcus and its nearness to the dividing fissure between the two hemispheres. Among several brain casts of Miocene carnivores, I have seen none which displays the crucial sulcus, though we can scarcely believe that this fissure, which is now so characteristic of the recent families of the order, had not then been developed.

One very striking difference between the cerebral sulci of *Cynodesmus* and those of the existing dogs, is the absence in the former of the posterior prolongation and downward curvature of the fissures. The medilateral is lacking, and a minute, isolated depression is all that can represent the ectolateral. Nor do I find any trace of the presylvian (supraorbital) sulcus, or of the "fissura anterior und postica," which, in the recent species, are always present and nearly always connected to form a strongly curved sulcus between the sylvian and the suprasylvian. It is of interest to note that this brain, in its simplicity of convolution, is much more like that of foetal dogs than of any adult recent species. Among existing carnivora, we find such simple sulci approximated only in some of the smaller viverrines and mustelines.

The cerebellum does not differ in any important respect from that of recent dogs, except that it is less extensively covered by the hemispheres. The vermis is prominent and well convoluted, and is principally extended upon the dorsal side. The lateral lobes are somewhat injured by weathering, so that the degree of their convolution is not apparent.

In the subjoined table, comparative measurements are given of the skulls of *Cynodesmus*, *Temnocyon coryphæus* and *Canis latrans*. Under each species, the first column gives the actual dimensions in millimeters, while in the second column are the proportionate measures, by Huxley's method, the length of the basicranial axis in each case being taken as 100. These figures are calculated only to the nearest integer, the fractions representing amounts which are far within the limits of individual variation.

	CYNODESMUS.		C. LATRANS.		T. CORYPHÆUS.	
	M.	AXIS = 100.	M.	AXIS = 100.	M.	AXIS = 100.
Length of basicranial axis.....	.066	100	.061	100	.066	100
Total length of skull.....	.147	223	.161	264	.153	234
Length of face.....	.048	73	.073	120	.056	85
Length of zygoma.....	.074	112	.072	119	.074	112
Width across zygomas.....	.106	161	.098	161
Length upper molar-premolar series.....	.052	79	.069	113	.055	83
Length of upper sectorial.....	.015	23	.020	33	.017	26
Width of upper sectorial.....	.011	17	.009	15	.011	15
Length of first upper molar.....	.011	17	.013	21	.010	15
Width of first upper molar.....	.016	24	.017	28	.016	24
Length of second upper molar.....	.007	11	.008	13	.004	6
Width of second upper molar.....	.010	15	.012	20	.009	14
Width of palate at <i>p. 4</i>043	65	.052	85	.050	76
Length of auditory bulla.....	.024	37	.023	38	.027	39
Length of mandible.....	.113	171	.130	212
Length of first lower molar.....	.017	26	.021	34
Length of second lower molar.....	.008	12	.010	16
Length of third lower molar.....	.005	8	.005	8

It should be added that, in *Cynodesmus*, the length given for the basicranial axis is approximate only, the margins of the foramen magnum being broken away, but the error cannot be sufficient to detract from the substantial accuracy of the results.

This beautiful specimen was found in the lower beds of Deep River valley by Prof. O. C. Morton.

THE SYSTEMATIC POSITION OF CYNODESMUS.

Of the phylogeny of the *Canidæ*, which has so long remained obscure and puzzling, Schlosser says: "Die Abstammung des Hundes ist noch immer mehr oder weniger in Dunkel gehüllt. Es sind zwar eine grosse Menge fossiler Fleischfresser

bekannt, die jedenfalls in näherer oder entfernter Beziehung zu dieser Gruppe stehen, allein da von denselben das Skelet entweder noch nicht gefunden ist oder doch von jenem der Hunde sehr bedeutend abweicht, so bleiben wir noch immer über die eigentlichen Ahnen des Hundegeschlechtes fast ganz und gar im Ungewissen" (No. 29, p. 247). The gradual recovery of the dogs of the American Miocene formations is bringing us nearer to a satisfactory solution of this difficult problem. As Schlosser has pointed out, the numerous cynoids of the European Oligocene, with the possible exception of some species of *Cynodictis*, can be of little phylogenetic significance, and in the lower Miocene of Europe the dogs disappear completely; they are represented in the upper Miocene and Pliocene by only a few remains, and do not attain great importance till the Pleistocene (No. 30, p. 488). Throughout the American Miocenes, however, from the White River to the Loup Fork, they play a very important part, and are not only abundant in individuals, but very varied in type, no less than nine genera of Miocene dogs, most of them containing several species, having been described from the different American horizons. This fact of itself would indicate the greater probability of an American rather than a European origin of the family.

In the Loup Fork beds, aside from the aberrant *Æluroidon*, several species of cynoids occur which are indistinguishable from *Canis*, and, so far as the remains at present known are concerned, must be referred to that genus, though complete material will probably require their separation from it. One of these species, *C. brachypus* Cope, is very probably of phylogenetic importance and is significantly like *Cynodesmus*. This is a microdont species, which retains many primitive characters, such as the small sectorials, short face, long cranium, elevated sagittal crest and weak feet. The lower Loup Fork strata of the Deep River valley (*Cyclopidius* beds) contain a possible species of *Canis*, the *C. ? anceps*, which will be hereafter described. So far as this form is known, it is intermediate between the *C. brachypus* and *Cynodesmus*. The latter genus is found in the lower Deep River beds, which we have already referred to the summit of the John Day horizon, and its connection with *C. brachypus* is a fairly close one, as is apparent not only in the dentition but in the characters of the skull as well; as, for example, in the characteristic shape and connections of the paroccipital processes, length of the zygomatic arches, size and shape of the coronoid process of the mandible, etc. We may also fairly assume that "the elevated sagittal crest and the small feet" are shared by the older genus. The White River type, *Daphænus*, is separated from *Cynodesmus* by a wider interval, the typical John Day horizon, in Oregon, not having as yet yielded any form which can be placed in the series, unless we are to find the missing link in the species

referred provisionally to *Temnocyon* by Cope, under the name of *T. josephi*; but until the mandibular dentition of that species is discovered, its place in the cynoid series must remain indeterminate. In spite, however, of the considerable gap between *Cynodesmus* and *Daphænus*, their relationship is indicated by nearly every detail of known structure in the two genera. The skull characters are closely similar in both; *e. g.*, the long, narrow cranium, with postorbital constriction placed far back of the orbits, and the short, rapidly tapering face. *Cynodesmus* shows advance over *Daphænus* in the following particulars: (1) The auditory bullæ are enlarged, fully ossified and the posterior chamber indistinguishably fused with the anterior, while in the White River genus the posterior chamber remains cartilaginous, or, at all events, is separate from the anterior. In all the skulls which I have had the opportunity of examining, the posterior chamber is lost, exposing the periotic from below, and the anterior chamber is very small. (2) The cranium is somewhat more rounded and capacious, and it, together with the zygomatic arches and ascending ramus of the mandible, has become somewhat shortened. (3) The sectorials are rather more modernized and efficient shearing blades, the cusps being more compressed and extended and less conical in form; in p. 4 the deuterocone is reduced. (4) The third upper molar has disappeared. (5) The first upper molar has become smaller and the outer cusps moved nearer to the edge of the crown.

Temnocyon represents a slightly modified side branch, in which the inferior sectorial has developed a trenchant talon, through the reduction or suppression of the entoconid. In all other respects, the true canine character of *Temnocyon* and its close resemblance in skull structure to *Cynodesmus* are very striking. Whether *T. coryphæus* and *T. altigenis* are properly placed in the same genus, or whether, as Schlosser suggests, they belong to widely separated phyla, need not be discussed here, nor can we determine at present whether *Temnocyon* and *Cynodesmus* have any common ancestor nearer than *Daphænus*. *Icticyon* alone, among recent dogs, shares with *Temnocyon* the character of the trenchant talon on the inferior sectorial. As this character is a rare one, both in fossil and recent cynoids, we may, perhaps, expect that the existing South American genus will prove to be derived from the John Day type. If so, many intermediate forms remain to be discovered.

Daphænus, in the structure of its skull, dentition and limbs, approximates closely to the creodonts. This approximation is seen in the character of the sectorials, which are very like those of the *Miacidæ*, in the primitive form of the cranium, in the low humeral trochlea with its epicondylar foramen, in the third trochanter of the femur, the creodont-like calcaneum and the relatively weak plantigrade feet. The cynoids of the Uinta formation are, unfortunately, not sufficiently well known for

generic or even ordinal reference, as it is uncertain whether they are carnivores or creodonts, but it is altogether likely that they will prove to be intermediate between *Daphænus* and the *Miacidæ* of the Bridger.

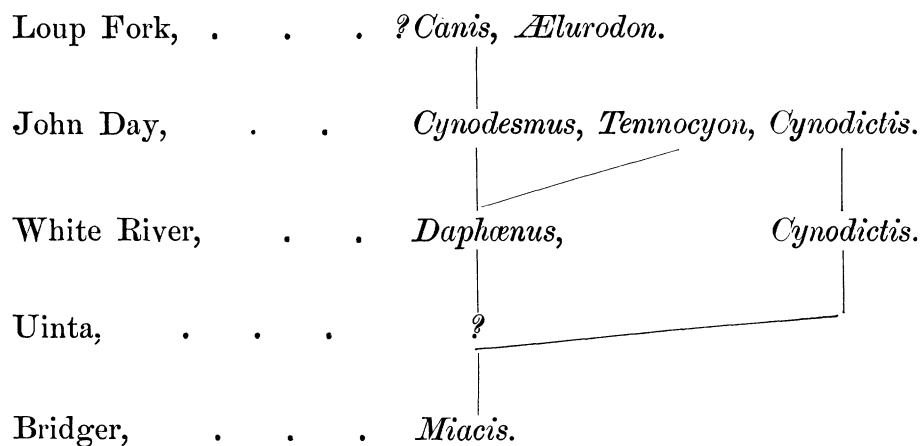
The great difficulty in the way of making out a satisfactory phylogeny of the *Canidæ* is the position to be assigned to the problematical genus *Otocyon*. If, as so many authorities maintain, it be inadmissible to assume that in this form the number of teeth has been increased at a comparatively recent period and within the limits of the family, then we shall be driven to admit a very remarkable degree of parallelism, or rather of convergence. Either the series of fossil forms which lead by slight and natural gradations from the *Miacidæ* to *Canis* have nothing to do with existing species, but merely form a parallel series, leading to no permanent result, while the real ancestors of the family are entirely unknown; or, on the other hand, *Otocyon* must represent the termination of a line leading upwards from some creodont family, as yet undiscovered, which line has paralleled the dogs in every detail of structure except the dentition. For my own part, I am by no means convinced of the impossibility of the addition of new teeth to the molar series. That modification in the mammalian lines is very generally by way of reduction in the number of teeth, is true, but does not prove that the reverse process may not exceptionally take place, whether by reversion or otherwise. The great simplicity of the teeth in *Otocyon* can hardly be reconciled with its advance in all other respects, except on the hypothesis of a retrogression or reversion in dental structure. At all events, such an assumption would seem to involve less of improbability than either horn of the dilemma to which its rejection confines us.

Stress has been laid upon the lyrate sagittal area of *Otocyon* and its occurrence in the young of other species of the family as showing that it is a primitive character. But an examination of a series of fossils in almost any mammalian phylum shows that the high and thin sagittal crest is the primitive character, and its replacement by a flattened area the secondary modification. The reason for this is plain; in the ancient forms, the jaws and canine teeth are powerful and the brain is small, hence the cranium does not offer sufficient surface for the attachment of the temporal muscles, and the sagittal crest must be developed, just as in the analogous case of the sternal keel in birds. Now, the disproportionately large size of the brain in the young animal gives a large surface for muscular attachment at a period when the weak jaws and small milk teeth require little muscular power, and hence the development of the crest is retarded. In no embryonic structure are there so many "cenogenetic" features as the skull, just on account of the great and premature enlargement of the nervous axis and the higher sense organs, and hence embryologi-

cal data must be applied with great caution in discussing questions of skull morphology. For the same reason, the sagittal crest is relatively less developed in very small forms, as is exemplified in the small species of *Cynodictis* from the White River and John Day, and in the least of these, *C. (Galecynus) lemur*, a lyrate area is formed, the most ancient known cynoid in which it occurs. A sagittal area also occurs in the White River insectivores, *Leptictis* and *Ictops*, but it is worthy of note that it is not marked in the older species of the latter, from the base of the Bridger.

There are equally good reasons for regarding the lobate mandible which is found in many of the recent *Canidæ* as a secondary modification. It not only is absent in all Miocene members of the family and all known creodonts, but, so far as I can ascertain, it occurs only in those recent species in which the mandibular condyle is much elevated above the level of the molars, and this is by no means a primitive character.

The following table will serve to display the relationships of the various American genera of the cynoid stem, so far as the available material renders this possible:



CANIS.

? CANIS ANCEPS Scott.

Amer. Naturalist, 1893, p. 660.

A small fragment of mandible, containing the last premolar, first and second molars, is provisionally referred to this genus. It agrees well with Cope's description of *Canis brachypus* from the Loup Fork (No. 4, p. 389), except for its inferior size and relatively more slender mandibular ramus. The inferior sectorial is nearly as long as in that species, in the proportion of 17 to 19, but the depth of the jaw beneath that tooth is much less, as 21 to 30. Possibly the species should be referred to *Cynodesmus*, but several minute details point rather to *Canis*.

The sectorial is very like that of *Cynodesmus*; it is marked by a very short (antero-posteriorly) paraconid and high conical protoconid, which has a very steeply inclined anterior edge; the talon, however, is somewhat more modernized by the increase in size of the entoconid, which bears about the same proportion to the hypoconid as in *Canis latrans*, and, as in that species, a minute cusp is present between the base of the metaconid and the entoconid, which does not occur in *Cynodesmus*. The second molar is like that of *C. latrans*, except for the larger size of the entoconid, which in the modern species is reduced to a mere ridge. The third molar is missing, but its alveolus shows it to have been larger than in the coyote, and the fragment of mandible displays a deeper and thicker horizontal ramus than in that species.

Measurements.

	M.
Length of first lower molar (antero-posterior).....	.017
Length of second lower molar.....	.008
Length of third lower molar alveolus.....	.006
Depth of mandible beneath <u>m. 1</u>021

The type specimen of this species was found in the *Cyclopidius* beds of the Deep River by Mr. I. Benet.

RODENTIA.

Castoridae.

STENEOFIBER.

This genus may be distinguished from the nearly allied *Castor* not only by the simpler pattern and less markedly prismatic character of the molar teeth, but also by the absence of coössification between the fibula and tibia. In the American species the humerus always has an epicondylar foramen.

STENEOFIBER MONTANUS Scott.

Amer. Naturalist, 1893, p. 660.

This species is most like the *S. (Castor) peninsulatus* Cope, from the typical John Day horizon, but differs from it in some details of molar construction. In the upper molars, except m. 3, there are but two fossettes, both of which are anterior to the external enamel inflection; the latter also is nearer to the posterior border of the crown than in the other species of the genus. In the lower molars there is, as in the other species, "a deep external enamel inflection and three transverse lakes on the inner side;" but different from any of the other members of the group, the external

inflection is hardly at all oblique in its course, but runs nearly parallel to the fore and aft axis of the tooth. In both of the lower teeth represented in the specimen, the antero-posterior diameter of the crown exceeds the transverse, which is very unusual in this genus. The incisors are narrow, with anterior faces which are less convex than in *Castor* and are covered with a thick layer of orange-colored enamel.

Two caudal vertebræ indicate that this species had a longer and more slender tail than the beaver; the anterior portion was provided with chevron bones.

The humerus has a rather slender, trihedral shaft and prominent deltoid ridge, which terminates in a massive overhanging hook; this hook is proportionately even better developed than in *Castor*. The supinator ridge is also conspicuous and continues high up upon the posterior aspect of the shaft. The trochlea is low and narrow, more so than in the beaver, but otherwise shaped as in that animal, and the anconeal fossa is very shallow, not so deep, in fact, as the supratrochlear. The internal epicondyle is very prominent, massive and rugose, and is perforated by a large foramen.

The femoral trochanters are well developed, but the third is placed more proximally than in *S. peninsulatus* or in the beaver. The calcaneum has a short, depressed, irregular and club-shaped tuber; the sustentaculum is notably smaller than in the modern species, and the external projection near the distal end much more prominent; the cuboidal surface is of triangular outline and slightly concave. Of the metatarsals only the third is preserved in the specimen, but this is sufficient to show that in this species of *Steneofiber*, at least, the foot had very different proportions from what we find in the existing genus. This metatarsal is relatively very much more slender and shorter than in *Castor* and of quite different shape, as the shaft is of nearly uniform size throughout, not being contracted in the middle nor expanded distally; it is also more depressed and flattened, and the head for the first phalanx less enlarged. The proximal end has an oblique surface for the ectocuneiform, which is abruptly constricted behind and continued as a narrow posterior tongue. This specimen suggests very strongly that when *Steneofiber* becomes completely known it will prove to be much better distinguished from *Castor* than the skull and dentition have led us to suppose.

Measurements.

	M.
Length of first upper molar.....	.004
Width of first upper molar.....	.005
Length of second upper molar.....	.004
Width of second upper molar.....	.005
Length of third upper molar.....	.003

Width of third upper molar.....	.004
Length of lower molar.....	.005
Width of lower molar.....	.004
Length of third metatarsal.....	.019

The specimen was found in the upper John Day beds of Deep River by Mr. C. C. Jefferson.

PERISSODACTYLA.

Equidæ.

The name *Anchitherium* has been very extensively applied to all those genera of American equines from the different Miocene horizons which have molariform premolars and short-crowned molars free from cement. Marsh was the first to suggest the removal of the American species from this genus (No. 26, p. 248, and No. 25, p. 249), and gave the names *Meshippus* and *Miohippus* to the species from the White River and John Day beds respectively, though retaining the older term for some forms from the latter group. However, the characters upon which these proposed genera were founded, are quite insufficient for the purpose, and hence they have not been widely adopted. Nevertheless, in my judgment, the separation may be justified upon very different grounds and the genera established upon significant structural characters. The distinction between *Meshippus*, on the one hand, and *Miohippus*, on the other, is still somewhat uncertain, though quite probable, but their common differences from *Anchitherium* are clear. The American genera may be confidently regarded as important members of the equine stem, while *Anchitherium*, from present information, would appear to belong to an abortive side branch, leading to no permanent results. The discovery in this country of a very large *Anchitherium* of the type of the European *A. aurelianense*, which will be described in the sequel, is somewhat unexpected and promises to be of twofold service, both in determining the morphological significance and systematic position of this genus and in correlating the upper Miocene horizons of the Old World and the New. The uncertainty which still attends the latter question is often a most serious obstacle in working out the problems of phylogeny, as well as in attempting to decipher the complex history of ancient migrations and to determine in what region a given type originated.

The following table will display some of the more important differences which separate the successive forms of horses occurring in the American Miocene formations, though there will, of course, be various opinions as to the taxonomic value of these characters.

I. Teeth brachyodont.

- A. Conules of upper cheek teeth well marked; posterior transverse crest not reaching the outer wall; external cusps moderately concave or flattened; anterior pillar of lower teeth distinctly marked.

1. No cement present.

- a.* Incisors without enamel invagination.....**Mesohippus*.
b. Upper incisors with enamel pit.....*Miohippus*.

2. Cement on cheek-teeth.

Posterior transverse crest of upper molars and premolars confluent with outer wall.....*Desmatippus*.

- B. Conules of upper cheek-teeth much reduced and external cusps deeply concave; posterior transverse crest extending to outer wall; anterior pillar reduced and on one or more lower teeth absent; no cement.....*Anchitherium*.

II. Teeth hypsodont.

1. Antero-internal cusp of upper cheek-teeth confluent with anterior crest.....*Protohippus*.
 2. Antero-internal cusp separate from transverse crest.....*Hipparion*.

MIOHIPPIUS Marsh.

American Journ. Science, Third Series, Vol. VII, p. 249.

(Syn. *Anchitherium* Leidy, Cope and Marsh, in part.)

This genus was proposed on the absence of the lachrymal fossa in the type species, but Prof. Cope informs me that this character is not of more than specific value, as in *Protohippus* and *Hipparion*, as well as in the John Day genus, some species have it, while others lack it. As shown in the foregoing table, *Miohippus* is sufficiently well distinguished from *Anchitherium*, but the propriety of its separation from *Mesohippus* must remain doubtful until the upper incisors of the latter genus have been found.

The John Day species have all been established on characters taken from the upper molars, and, as there are no upper teeth comprised in the present collection, the reference of the species can only be approximate.

MIOHIPPIUS EQUICEPS? Cope.

(Syn. *Anchitherium equiceps* Cope, *Proceedings Philos. Soc.*, Vol. XVIII.)

The lower beds of the Deep River (*i. e.*, upper John Day) yielded some mandibles which agree fairly well with the smaller individuals of this species, to which they may be provisionally referred.

*The upper incisors of this genus are not known, and future discovery may show that it is not generically different from *Miohippus*, but the generally less advanced character of the dentition renders it probable that the character of the incisors is as assumed above.

MIOHIPPIUS ANNECTENS? Marsh.

(Pl. I, Figs. 6-8.)

(loc. cit.)

A fine specimen of a hind limb from the lower beds, not accompanied by teeth, corresponds closely to the measurements given by Marsh of this, the type species of the genus. The femur differs little, except in size, from that of *Mesohippus*; it is relatively longer, more nearly equalling the length of the tibia. The head rises as much above the bridge which extends to the great trochanter, but is more approximated to that process, and the pit for the round ligament is wider and more equine in shape. The head projects to a remarkable extent in front of the anterior plane of the shaft. The shaft is laterally compressed, and narrow when seen from the front, but of considerable antero-posterior diameter. The pit above the external condyle for the attachment of the plantaris muscle is very deep and conspicuous. The condyles are rather small and do not project strongly backward, but are more prominent and separated by a deeper groove than in *Mesohippus*. Another difference from the latter genus is seen in the greater elevation and thickening of the inner border of the rotular trochlea, though this by no means attains the proportions found in *Equus*.

The tibia is almost an enlarged copy of that of the White River genus. The condyles for the femur are brought somewhat closer together and extended farther backward and the enemial crest is rather more prominent; the shaft is rather stouter and the distal end more expanded. The inner malleolus is more massive and the grooves for the astragalus somewhat more deeply incised; the inner groove exceeds the outer in antero-posterior extent in a more marked degree. About two inches of the distal end of the fibula is firmly coössified with the tibia, forming a stout external malleolus, which bears a small facet for the calcaneum. The proximal portion does not appear to have coalesced with the tibia, and is lost; nor can we determine whether the exceedingly slender shaft was interrupted.

Beyond the mere increase in size, the tarsus shows surprisingly little advance over that of *Mesohippus*. The calcaneum retains the long, slender tuber with nearly parallel dorsal and plantar borders; the distal part is a very little shorter in proportion, so little that the difference is probably individual. The cuboidal facet is longer, more distinctly separated into anterior and posterior portions, and the latter is more incurved toward the sustentaculum, which constitutes an advance toward the modern standard. The other facets show no change.

The astragalus likewise presents no noteworthy differences other than the extension of the distal end, especially towards the tibial side. The small sulcus which is very generally, though not invariably, found on the navicular surface in *Mesohippus*,

does not occur in the specimen, but in all probability this is an individual, or, at most, a species character.

The navicular is a little lower relatively, and has also increased in transverse breadth, more particularly towards the internal or tibial side. The posterior margin of the astragalar surface is less elevated and less widely notched, and the posterior projection which extends towards the cuboid is less prominent. As in the case of the astragalus, the corresponding sulcus is absent. On the distal side, the facet for the ectocuneiform has increased in size, and that for the combined meso- and entocuneiforms has become somewhat more posterior in position. The anterior face of the navicular is decidedly less curved.

The cuboid has slightly increased its dorso-plantar diameter and the posterior hook has become decidedly more massive and rugose, even more so relatively than in *Equus*. The astragalar surface is wider, and the hinder part of the calcaneal facet broader, more incurved and more equine in shape.

The ectocuneiform is broader and lower, but otherwise as in *Mesohippus*. Although the animal was fully adult, the suture between the ento- and mesocuneiforms is very clearly shown, much more so than in any White River specimen which has come under my observation, and the ankylosis of the two elements appears to be a somewhat loose one. This, again, is doubtless an individual character. The entocuneiform in both genera extends across to a contact with the cuboid, though in *Miohippus* it is relatively larger, especially in vertical diameter. The navicular facet on the mesocuneiform is somewhat more concave and rises higher behind.

In the metatarsals, the only noteworthy change is in the increase in size of the median one, though its articulations remain as before; it is still excluded from contact with the mesocuneiform by the junction of the second metatarsal with the ectocuneiform, which is very limited.

Measurements.

	M.
Length of femur225
Width of distal end (transverse)047
Depth of distal end (fore and aft)057
Length of tibia.....	.263
Width of proximal end.....	.050
Depth of proximal end.....	.048
Width of distal end (including fibula).....	.037
Depth of distal end at inner astragalar groove.....	.026
Length of calcaneum.....	.068
Length of astragalus.....	.032
Width of astragalus head.....	.022
Width of proximal end of third metatarsal.....	.020
Depth of proximal end of third metatarsal.....	.016

This specimen was found by Prof. W. F. Magie in the lower beds of the Deep River valley.

MIOHIPPIUS sp.

What is probably a third species of this genus is represented by teeth and limb bones from the *upper* beds (lower Loup Fork), the specific reference of which is uncertain in the absence of the characteristic upper molars. In size, this animal about equals the *M. (Anchitherium) brachylophus* Cope from the John Day, and is therefore one of the smaller forms which exceed *Mesohippus* in stature but relatively little. Fragmentary as they are, these remains are of interest as showing the degree in which some members of a genus may retain their primitive characteristics, while descendants of the same genus have already advanced far on the road of specialization. To make clear the position of these late survivors, it will be most convenient to compare the specimens with the corresponding parts of *Mesohippus*, than which they are distinctly more modernized, though perhaps less than we should have expected.

The humerus has a somewhat more rounded and less laterally compressed shaft. The trochlea is decidedly more equine, lacking the peculiar flange which I have elsewhere described as occurring on the external side of the humeral trochlea in the White River genus. This external surface is continued much farther back upon the distal aspect of the trochlea, and thus there is not that conspicuous difference in vertical diameter between the external and internal portions of the trochlea which gives such a peculiar and characteristic appearance to the humerus of the older form. It should be added that the humerus of this species is more modernized than that of the John Day members of the genus, which still display some traces of the arrangement found in *Mesohippus*. Returning to the species under description, we find that the intertrochlear ridge is reduced, but is still much more prominent than in *Equus*, and the sulcus, which in the latter is placed at the bottom of the intertrochlear groove, is on the summit of the ridge; in *Mesohippus* it is wanting. The inner portion of the trochlea has its articular surface reflected farther back on the upper side than in the horse, which indicates a greater freedom of motion at the elbow joint. The internal epicondyle is reduced and, seen from this side, the distal end is a reduced copy of that of *Equus*.

Except for the position of the bicipital tubercle, which is still internal rather than anterior, the head of the radius is much more equine in appearance than that of *Mesohippus*. Not only is the peculiar external flange absent, but the head is wider and expanded much as in the horse. The shaft is likewise more flattened antero-

posteriorly and broadened transversely. The distal end, however, retains its trihedral shape and the carpal facets differ in no important respect from those of the White River form. The distal end of the ulna is coössified with the radius to about the same extent as frequently, though not always, occurs in the latter.

The carpals exhibit numerous differences of detail from those of *Mesohippus*, many of which are to be correlated with the increase in size of the median digit. In general, the most noticeable change in the carpus is the increased breadth and decreased proportionate height of its elements. The scaphoid is broader and deeper (antero-posteriorly) relatively to its height, and on the radial surface the anterior ridge is higher and the posterior concavity deeper. The external contour of the radial facet is more deeply notched. The lunar differs in the greater width of the distal as compared with that of the proximal end, and the more nearly square outline of the radial surface, which is less contracted posteriorly. The magnum facet is also carried farther back. In these respects the lunar of the species before us is less equine than that of *Mesohippus*. On the other hand, it is more modernized in the greater breadth of the surface for the magnum in proportion to that for the unciform and in the open angle at which the two facets meet. The pisiform is more equine in being more expanded vertically and of more uniform height, contracting less towards the proximal end. The cuneiform facet is more oblique, presenting less downward and more forward, but is still only imperfectly divided into two parts. The trapezoid is very similar in the two genera. The magnum is much broader, especially anteriorly; this extension is chiefly towards the radial side and consists principally in a broadening of the scaphoid surface. Distally, we find the expansion for the median metacarpal more symmetrically formed on both sides of the posterior prolongation. The head of the magnum remains, as before, very narrow.

In the metacarpus the only noteworthy change is the expansion of the median and reduction of the lateral digits; in consequence of this, the magnum surface on mc. iii is decidedly changed in shape. The other carpal facets of the metacarpus remain very much as before. Mc. ii has the same connections with trapezium, trapezoid and magnum, and mc. iii with magnum and unciform, the latter facet being divided into two parts by a sulcus, which is somewhat better marked than in *Mesohippus*.

Measurements.

	M.
Breadth of humeral trochlea.....	.035
Length of radius.....	.159
Breadth of proximal end.....	.031
Breadth of distal end.....	.038
Width of head of mc. iii.....	.016
Depth of head of mc. iii.....	.014

DESMATIPPUS Scott.

Amer. Naturalist, 1893, p. 661.

Equines in which the dentition is intermediate in character between that of *Miohippus* and that of *Protohippus*. The molars and premolars are short crowned and have the valleys more or less filled with a thin deposit of cement. In the upper series, the posterior transverse crest is connected with the outer wall, and in the middle of its course sends forward a process which extends nearly to the anterior conule. The posterior pillar is enlarged, and on moderate wear becomes confluent with the postero-internal cusp. In the lower cheek-teeth the internal cusps are reflected and expanded antero-posteriorly, so as to narrow the entrances to the valleys. The median inner cusps (*a a'* of Rüttimeyer) are much more distinctly separated than in *Anchitherium* or *Miohippus*.

DESMATIPPUS CRENIDENS Scott.

(Pl. II, Figs. 9-14.)

(*loc. cit.*)

Size moderate; limbs elongate and slender; posterior transverse crests of upper cheek teeth crenulate.

This interesting genus fills very completely and satisfactorily what was almost the only gap left in the equine phylum, viz., that between *Miohippus* and *Protohippus*. At first sight it might seem to be identical with the *Merychippus* of Leidy, but this genus was established upon two upper milk molars (No. 23, Pl. XVII, Figs. 3 and 4) of peculiar construction, the reference of which is still entirely uncertain. The permanent dentition which Leidy has referred to this genus differs altogether from that of *Desmatippus*, being much more like that of *Protohippus*, with which Cope identifies it.

The type specimen of the new genus consists of the dentition of both jaws, lacking the incisors, canines, first lower premolar and last upper molar, the mandible, portions of the radius and ulna, femur, manus and pes, and fragments of other bones. Other specimens, which should probably be referred to the same genus, though perhaps a different species, will be described in the sequel.

Dentition. A. Upper Jaw. The first premolar, though much smaller than the others, is relatively large and well developed, and is composed of four elements. The protocone, which is much the largest, is elongate, somewhat convex upon the outer face and displays a rounded projection upon its inner face. The tritocone is small, not very distinctly separated from the protocone, and is overlapped by the greatly extended anterior buttress or protostyle of p.². The deuterocone is represented by a

long, low ridge, which is not connected by a transverse crest with the outer wall of the crown. The tetartocone is low and conical in shape; on wear it becomes confluent with the tritocone. Strange to say, this tooth is proportionately less reduced than in the White River equine, *Meshippus*. The second premolar is the largest tooth in the series and differs in several details of construction from all the others; the enlargement affects particularly the anterior portion of the crown. The protocone (antero-external cusp) is elongate in the antero-posterior direction; it is but very slightly concave and the median rib is prominent. The protostyle, or anterior buttress, is greatly enlarged, and to it much of the characteristic appearance of the tooth is due. The tritocone is much shorter (from before backward) than the protocone, is more concave on the external side, and the median rib is nearly obsolete. The deutocone is fused with the anterior conule, though a constriction indicates clearly the limits between them, and the thickness of the conule renders it a very conspicuous element of the crown; the anterior transverse crest is approximated to, but does not coalesce with, the outer wall. The tetartocone is somewhat less distinctly constricted from the large and prominent posterior conule, and this makes the posterior transverse crest very much broader than in *Anchitherium*; it is confluent with the outer wall, and the enamel on its anterior margin is slightly crenulate. The posterior pillar is large and of triangular shape; in the stage of wear exhibited by the specimen, the pillar has become confluent with the tetartocone, though the limits of the two cusps are marked by a fold in the enamel covering. A small pillar or style arises also from the anterior side of the tetartocone, but doubtless this, as in *Anchitherium*, is an individual character. Although this tooth is typically brachyodont, cement is deposited in the anterior and posterior valleys, but apparently not in the median valley or the outer or inner sides of the crown.

The third and fourth premolars differ from the second chiefly in matters of detail. The proto- and tritocones are of more nearly equal size and shape, though the former still exceeds the latter in size; it is somewhat concave on the external face and the median rib is obsolete. The posterior crest is angulate and sends forward a process which nearly reaches the deutocone; its front margin, especially on p. 4, is much more markedly crenulate than in p. 2.

The molars decrease in size from the first to the third; their construction closely agrees with that of the premolars, but the external cusps (para- and metacones) are of nearly equal size and less concave than the corresponding elements of the premolars. The conules, especially the anterior, are somewhat more separated from the inner cusps. The posterior transverse crest is confluent with the outer wall, but the anterior is not.

As compared with the upper molars of the large European *Anchitherium*, *A. aurelianense*, those of *Desmatippus* differ in the following respects: (1) The presence of cement in the valleys; (2) the great widening of the transverse crests, especially of the posterior ones; (3) the much greater distinctness of the conules, which in the European species are very obscurely marked; (4) the greater flatness of the external cusps.

B. Lower Jaw. The first premolar has been lost from the specimen. The second differs considerably from the others in the shape of the anterior half of the crown; this portion of the tooth is flattened on the outer side and tapers anteriorly, giving it a wedge-like shape, when viewed from above. In consequence of this arrangement, the protoconid is triangular in section, the crests to the para- and deutoconids respectively straight instead of curved, and the external valley is wider and of a different shape from that of the other premolars; the paraconid is larger and the posterior pillar smaller. Seen from the outside, this tooth appears to have a very similar construction to the $\overline{p.2}$ of *Mesohippus*, but in a crown view the following differences are to be observed: (1) The proto- and paraconids are connected by a crest; (2) the anterior internal valley is very much better developed; (3) an anterior pillar is formed behind the deutoconid, though both of these elements are much smaller than in the other premolars. In *Anchitherium aurelianense* the development of this tooth has proceeded farther than in *Desmatippus*, but in a somewhat different and peculiar way, the paraconid being greatly enlarged, comparable to the very large anterior buttress of the corresponding upper tooth.

The third and fourth premolars are molariform. The paraconid is much reduced and not distinguishable as a separate element from the anterior crest; the deutoconid and anterior pillar are enlarged and of nearly equal size, and though much less distinctly separated from each other than in *Protohippus*, they are sufficiently enlarged to narrow the entrances to the internal valleys, which expand on the external side of them; the posterior pillar is fairly well developed and, when moderately worn, becomes confluent with the tetartoconid. The latter cusp is simple and does not send forward a crest such as is found in *Protohippus*.

The molars, as in the upper jaw, decrease in size, especially in breadth, posteriorly, $\overline{m.3}$ being conspicuously narrower than $\overline{m.1}$ and, but for its talon, shorter as well. In construction they differ but slightly from the premolars. On $\overline{m.1}$ the posterior pillar is rather smaller than on $\overline{p.4}$, and on $\overline{m.2}$ it appears to be wanting, but $\overline{m.3}$ shows it enlarged and developed into a distinct heel. None of the lower teeth in the type specimen display any indubitable traces of cement; other isolated teeth, however, which I think should be referred to the same genus, if not the same species, have a very thin coating of this substance.

Measurements.

	M.
Upper molar-premolar series, length.....	.117
Upper premolar series, length.....	.068
Upper first premolar, length.....	.014
Upper first premolar, width.....	.009
Upper second premolar, length.....	.022
Upper second premolar, width.....	.019
Upper third premolar, length.....	.019
Upper third premolar, width.....	.020
Upper fourth premolar, length.....	.019
Upper fourth premolar, width.....	.020
Upper molar series, length.....	.049
Upper first molar, length.....	.018
Upper first molar, width.....	.020
Upper second molar, length.....	.016
Upper second molar, width.....	.018
Upper third molar, length.....	? .014
Upper third molar, width.....	? .017
Lower molar-premolar series, length.....	? .119
Lower premolar series, length.....	? .066
Lower second premolar, length.....	.019
Lower second premolar, width.....	.003
Lower third premolar, length.....	.0185
Lower third premolar, width.....	.010
Lower fourth premolar, length.....	.017
Lower fourth premolar, width.....	.011
Lower molar series, length.....	.053
Lower first molar, length.....	.018
Lower first molar, width.....	.010
Lower second molar, length.....	.016
Lower second molar, width.....	.009
Lower third molar, length.....	.018
Lower third molar, width.....	.007
Depth of mandible below $\overline{m. 1.}$? .032
Depth of mandible below $\overline{m. 3.}$047
Height of condyle.....	.103
Breadth of angle to $\overline{m. 3.}$068

The horizontal ramus of the mandible is, for the most part, slender and shallow, especially towards the symphysis; but as the inferior border is nearly straight, and the line of molars rises rapidly posteriorly, the jaw becomes quite deep beneath $\overline{m. 3.}$ The ascending ramus is high and the condyle is placed much above the level of the molars. The angle is rounded and not prominent. The anterior border of the ascending ramus is almost straight, broad and slightly grooved, the *linea obliqua externa* being better developed than in the horse, but less so than in the more ancient genera. My attention was called to this interesting transitional character by my

assistant, Mr. Graham, and on further examination I find it to be frequently the case in other phyla, that the breadth of this border and the depth of the groove diminish in the more modernized forms.

The radius has a slender, flattened shaft, which expands distally and is also much thickened antero-posteriorly, so as to be of trihedral section. In this respect, *Desmatippus* resembles the less advanced genera and differs in a marked way from *Protohippus* and the later forms. The distal thickening is entirely on the anterior face, the posterior side remaining flat or even slightly concave. The distal ends of the radius and ulna are firmly coëssified for a length of about two inches; above this, the shaft of the radius has upon its postero-external edge a shallow and narrow groove for the shaft of the ulna, which was obviously very slender, though probably not interrupted. The carpal surfaces of the forearm bones are too much mutilated for description.

Of the metacarpals, the third is preserved entire and also portions of the second. The former is remarkable for its slenderness and length, in which latter respect it considerably exceeds that of *Protohippus sejunctus*. Unfortunately, the proximal articular surfaces are so much broken that they cannot be made out satisfactorily. The distal end exhibits some important features which are intermediate between the more ancient and the later genera. As in the former, the shaft is expanded transversely just above the trochlea, which is narrower, while in *Equus* the trochlea is wider than any portion of the shaft. As compared with the earlier forms, the trochlea is higher and the carina, which in all preceding genera is confined to the palmar side, is in *Desmatippus* continued over the entire anterior face of the articular surface; very faintly, it is true, and yet unmistakably. This genus is therefore the first, at least in the direct line of descent, in which this characteristic equine feature appears.

The character of the phalanges will be best explained after quoting Kowalevsky's comparison between those of *Anchitherium* and *Equus*: "Par la forme des phalanges l'*Anchitherium* diffère complètement du cheval et de l'hipparion; il lui manque ce rétrécissement si considérable qui est caractéristique pour la première phalange des équidés; les phalanges du *Daw* qui ont 69 mm. de long. présentent au milieu une largeur transverse de 25 mm., tandis que les phalanges de l'*Anchitherium* qui n'ont que 35 mm. de longueur, c'est-à-dire la moitié, présentent au milieu une largeur transverse plus considérable, 26 mm." (No. 20, p. 66).

In *Desmatippus* the proximal phalanx of the median digit has already attained proportions which closely approximate those seen in *Equus*. The relative breadth of the proximal and distal ends is almost the same as in the horse, but the contrac-

tion of the bone in the middle is less marked. The groove for the metacarpal carina is deep near the palmar side; dorsally it becomes very faint, but is continued across the entire proximal surface and very slightly notches the anterior margin. On the palmar side of the phalanx the triangular roughened area for the attachment of the inferior sesamoid ligament, which in the horse descends nearly to the distal trochlea, is in *Desmatippus* very much smaller and confined to the proximal portion of the bone. The distal articular surface is less convex than in the horse, and is less reflected upon the dorsal and palmar sides; upon the latter side its margin is interrupted by a notch, which, however, is not so long or so deep as in the modern genus. The second phalanx is longer and more slender proportionately than in the horse, and is also more depressed and flattened than in that animal; the proximal articular surface is less concave, its median ridge less pronounced, and the tubercles for the attachment of the lateral interphalangeal ligaments are but slightly developed. The distal articular surface is not reflected so far upon the dorsal side as in *Equus*, though on the plantar side it rises as high relatively and the surface for the so-called navicular sesamoid is well marked. The ungual phalanx is only partially preserved, but enough remains to show that it is more equine in character than the long, depressed and flattened ungual of *Anchitherium aurelianense*. The line of the dorsal surface descends more steeply than in that species and the front margin of the proximal surface is elevated in the median line to form a slightly recurved, hook-shaped process, which, though much less prominent than in the horse, is much more so than in *A. aurelianense*.

The lateral digits, so far as can be judged from the fragmentary remains, were still fairly developed, and though much more reduced than in *Miohippus*, appear to be somewhat less so than in *Protohippus*. The distal trochlea of the metacarpal is less developed in proportion to the breadth of the shaft than in the John Day forms.

Measurements.

	M.
Metacarpal iii, length185
Metacarpal iii, width of proximal end020
Metacarpal iii, width of distal end018
Metacarpal ii, width of distal end009
Metacarpal ii, depth of distal end015
First phalanx iii digit, length050
First phalanx iii digit, width of proximal end024
First phalanx iii digit, width of distal end020
Second phalanx iii digit, length020
Second phalanx iii digit, width of proximal end024
Second phalanx iii digit, width of distal end021
Third phalanx iii digit, width of proximal facet022

A fragment of the pes accompanies the type specimen, which, however, displays no features of especial interest, as the bones are not sufficiently well preserved to show the minor changes in the articulations, which are so important in the equine series. As in the American genera of this series, the ento- and mesocuneiforms are coössified, not as in the European species of *Anchitherium*, the ecto- and mesocuneiforms. The internal cuneiform is very large, and forming nearly a right angle with the median, extends beneath the entire plantar border of the navicular to the cuboid. The ectocuneiform is higher vertically, in proportion to its breadth, than in *Protohippus*. The proximal portion of the median metatarsal is rather slender and rounded; that of the laterals is surprisingly large antero-posteriorly, but in part, at least, this is due to crushing. The shaft of the laterals rapidly tapers and becomes very slender. The median metatarsal appears to have a slight contact with the mesocuneiform, but the specimen is too imperfect to determine this point with certainty.

A second specimen, consisting of the tarsus and portions of the metatarsus, should probably be referred to this genus, though possibly representing a different species. It differs from the fragmentary pes belonging to the type specimen in only one particular, viz., in the much narrower proximal end of mt. ii. Part of this difference is no doubt due to the crushing to which the type specimen has been subjected, but not all of it, and the remainder may be referred to either individual or specific variation. Compared with the tarsus of *Protohippus sejunctus*, which Prof. Cope has kindly lent me for the purpose, some not unimportant divergences may be observed.

In size and general appearance the two specimens closely coincide; the differences are in matters of minute detail and are especially to be found in the relative development of the various facets. On the calcaneum attributed to *Desmatippus* the additional facet which runs distally from the ectal astragalar facet is somewhat longer than in *Protohippus*, but is not so clearly demarcated from the main facet. As in the latter, the ectal astragalar facet is in contact with that on the sustentaculum, but this latter surface is considerably broader and more nearly perpendicular to the long axis of the bone. The cuboidal surface is shorter, less distinctly divided into two parts, and at the plantar end less incurved, and is thus separated by a wider interval from the sustentacular facet.

The astragalus displays corresponding differences. The notch for the ectal calcaneal facet is wider and its distal continuation longer; from the latter the inferior border rises abruptly and terminates, as in *Equus*, in the beak formed by the sudden termination of the external astragalar condyle. In *Protohippus sejunctus* there is no such beak, but the outer condyle curves gently and without interruption into the external plantar border and the accessory calcaneal facet. Whether this is true of

all species of the genus, I cannot at present determine. Another difference from the astragalus of *Protohippus* is found in the more abrupt truncation of the proximal end of the outer condyle, which thus exposes upon the calcaneum a larger surface for the fibula. As in the corresponding facet of the calcaneum, the sustentacular surface is broader. The navicular surface descends less upon the external side and is separated by a less pronounced angle from the cuboidal facet, which is less extended. The sulcus which invades the navicular surface in both genera is much less conspicuous than in *Equus*.

The proximal surface of the cuboid is very similar in the two specimens, except that in *Protohippus* the posterior extension of the calcaneal facet is somewhat longer and more recurved towards the tibial side. The distal end, on the other hand, is quite different in the two. In *Protohippus* the facet for metatarsal iv is distinctly larger, and that for mt. iii less oblique and more distal in position, than in *Desmatippus*; in the latter the surface for mt. iii is rather lateral than distal, which is an ancient character.

The navicular is quite different from that of *Protohippus*; it has a notably greater vertical height and its antero-external angle is much more extended across the face of the cuboid, though far less so than in the horse. Both specimens differ from the latter in the broader posterior portion of the navicular, the relatively greater fore-and-aft diameter of the astragalar surface and in the much less conspicuous development of the beak-like plantar extension. The sulcus on the astragalar facet is also much less marked.

The enlarged ectocuneiform is very much alike in the two Loup Fork genera. Both differ from *Equus* in the more rounded and less extended posterior beak; the articular surface of mt. iii on this extension is continuous with the anterior one, being interrupted by a sulcus on the external side, not, as in *Equus*, isolated completely.

The coalesced meso- and entocuneiforms are much larger in *Desmatippus* and extend across to the cuboid, with which the internal element is in contact, while in *Protohippus* they are widely separated and the entocuneiform is much more reduced than in the horse. Both specimens display a minute facet for mt. iii on the middle cuneiform, but the surface for mt. iv is almost confined to this bone and extends but slightly to the internal one, while in the horse it does so largely.

In the metatarsals the differences are slight, so far as the materials permit a comparison. The cuboidal facet on mt. iii is more oblique and the head of mt. ii is less reduced in *Desmatippus*. Compared with *Equus*, more important divergences may be noted; the cuboidal facet of mt. iii is, in the older genus, much smaller and less proximal in position, and that for the mesocuneiform is also smaller; the posterior

surface for the ectocuneiform is much less developed and less completely separated from the anterior portion by the transverse sulcus. On mt. ii the surface for the entocuneiform is much less conspicuous.

The type of the genus was found by Mr. Benet.

The Systematic Position of Desmatippus.

Morphologically, there can be no doubt that this genus stands exactly intermediate between *Miohippus* of the John Day and *Protohippus* of the Loup Fork, and fills up the gap which has hitherto existed between those genera. This intermediate position is especially clear in the structure of the teeth. *Desmatippus* shares with *Miohippus* the short-crowned molars, and with *Protohippus* the presence of cement and the confluence of the posterior transverse crest with the outer wall in the upper teeth, and in the lower teeth the extension of the inner cusps and narrowing of the entrances to the internal valleys, though these features are less conspicuous. From these molars to those of the relatively short-crowned species of *Protohippus* the transition is an easy one. The same intermediate character is shown in the limbs and feet, so far as they are known, save only the greater length and slenderness of the metapodials, as compared with those of the more differentiated genus. These are, however, but specific, as distinguished from generic, characters and have but little importance.

An apparently strong objection to the position which I have assigned to this new equine genus may be drawn from the stratigraphical fact that it has as yet been found only in association with *Protohippus*. But, as we have already seen, there is a marked break between the faunas of the lower Deep River beds (*i. e.*, upper John Day) and the upper beds of the same region (*i. e.*, lower Loup Fork). With a few possible exceptions, no species of mammal is common to the two horizons and the great majority of the genera are different also. This abrupt change points with great probability to a hiatus between the formations, and in this case we may well believe that *Desmatippus* originated during the unrecorded period, and, after having given rise to *Protohippus*, persisted into the Loup Fork, just as *Miohippus* has done. Were the John Day beds unknown, we should have precisely the same difficulty with regard to the latter genus. Should this supposed unconformity prove not to exist, we must then assume that the later fauna was developed in some other part of the continent and reached the Montana valley by a migration. This assumption would dispose of the difficulty equally well.

So many cases of the apparent conflict between stratigraphical and morphological facts have been removed by further investigation, that we may confidently expect the same of this.

PROTOHIPPIUS Leidy.

Proc. Acad. Nat. Sci., Philadelphia, 1858, p. 26.

PROTOHIPPIUS SEJUNCTUS Cope.

Bull. U. S. Geol. and Geogr. Surv., No. 1, 1874, p. 13.

This specimen was found by Prof. Cope's collector in the Deep River beds, and is represented in our collection by a number of teeth and limb bones, which add nothing to our knowledge of the species.

PROTOHIPPIUS sp.

(Pl. II, Fig. 17.)

A smaller species than *P. sejunctus* is indicated by several specimens, none of which, unfortunately, are associated with teeth, so that we cannot tell whether they should be referred to any of the species from the typical Loup Fork horizons. The most characteristic specimen consists of the distal part of the ulno-radius, the proximal row of carpals and the heads of mcs. iii and iv. The radius may at once be distinguished from that of *Desmatippus* by the more equine shape of the distal portion, where the shaft is more flattened and less trihedral, with relatively greater transverse and less antero-posterior diameter. The ulna, the distal end of which, at least, is coössified with the radius, is more reduced than in *Desmatippus*, and, judging from the marks on the shaft of the radius, the shaft was interrupted.

Comparing the carpus of this specimen with that of *Miohippus*, we may observe important advances and modernizations. In the scaphoid, the width and antero-posterior depth are relatively increased; the proximal articular surface is reflected upon the palmar side, where it forms a small facet, articulating with a corresponding one on the radius in extreme flexion. That the trapezium was present is shown by a small facet on the scaphoid. The lunar has increased in dorso-palmar diameter and the posterior knob, which in *Miohippus* is a mere knob and does not carry any of the magnum facet, is very much more prominent and the distal facet is extended upon it, so that the latter has gained much in extent from before backward. The cuneiform is like that of *Equus* in almost every respect, except that it is more compressed and less massive, the upper pisiform facet is somewhat larger and the lower somewhat smaller. The pisiform is decidedly more equine than that of *Miohippus*, both in its much greater vertical height and in the separation of the two cuneiform facets, which in the latter are still connected. It has not attained, however, the full vertical diameter seen in the horse.

The median metacarpal is much expanded, and especially the palmar portion is

much wider than in *Miohippus*. The magnum surface is entire, and that for the unciform is larger and more oblique. This latter facet is divided into two parts by a sulcus, which hardly more than emarginates that for the magnum. It seems probable that a rudiment of the fifth metacarpal was preserved, for which a facet shows on the head of mc. iv.

Measurements.

	M.
Breadth of radius and ulna, distal end.....	.035
Depth of radius, distal end.....	.018
Height of lunar.....	.015
Width of lunar, distal end.....	.012
Width of unciform facet.....	.004
Width of mc. iii, proximal end.....	.021
Depth of mc. iii, proximal end.....	.014

Found in the upper beds of Deep river by O. C. Morton.

ANCHITHERIUM von Meyer.

Teeth brachyodont, without cement; upper molars and premolars with the posterior transverse crest confluent with the outer wall of the crown; conules so much reduced as to be scarcely distinguishable from the remainder of the crests; external crescents deeply concave and overhanging; in the lower cheek teeth the anterior pillar is reduced, and on more or fewer of the teeth is wanting; posterior pillar also reduced; incisors, either the upper alone, or both upper and lower, with shallow pits.

Whether the coössification of the meso- and entocuneiforms is a generic character remains to be seen.

ANCHITHERIUM EQUINUM Scott.

Amer. Naturalist, 1893, p. 661.

This animal may be at once distinguished from all other American horses by the generic characters given above, since this is the only known American species of *Anchitherium* in the restricted sense in which I have used that term. From the best-known European species, *A. aurelianense*, it differs in the following respects: (1) Larger size of the teeth in proportion to the skeleton; (2) absence of enamel invaginations in the lower incisors; (3) smaller size of the antero-external buttress on p. 2; (4) the transverse crests of the upper molars and premolars are less sinuous; (5) p. 2 has the anterior half of the crown flattened on the outside and no external valley; (6) the diastema between the lower canine and p. 1 is relatively shorter and the symphysis much narrower; (7) the proximal end of the humerus differs in details

that will be explained in the full description; (8) the median digit is more enlarged and its ungual phalanx shorter and more rounded, but also flatter and more depressed.

The type specimen of the species consists of a fragmentary skull (with the dentition almost complete), several vertebræ from different regions, the fore limb (lacking the scapula) and the pelvis. Several other fragmentary specimens are referable to the same species.

Dentition. A. Upper Jaw (Pl. III, Fig. 24). The incisors decrease regularly in their dimensions from the first to the third; they have very short, but broad and thick crowns, and already present a decidedly horselike appearance; the cingulum is elevated, and thus between this structure and the front margin of the crown a pit is formed. In spite of the fact that this genus, as will be shown in the sequel, is almost certainly not in the direct line of equine descent, we may conclude with great probability that these teeth explain the genesis of the invagination in the incisors of the recent horses and that, in the latter, the hind wall of the pit is to be regarded as a greatly enlarged cingulum. The canine has been lost, but the alveolus shows that it was rather small and separated from the incisors by a short diastema and from p.1 by a longer one.

The first premolar, as in the European species, is relatively larger than in the more ancient genera of the phylum, *e. g.*, *Mesohippus*. On the outer side it is convex and so obscurely divided that a tritocone can hardly be said to be present; the deuterocone is a long, low ridge, ending posteriorly in a cone, which probably represents the tetartocone in an incipient stage. As in the horses generally, the second premolar is the longest tooth in the series. This elongation from before backward is due to the enlargement of the antero-external buttress, or protostyle, which, however, is less extreme than in *A. aurelianense*; it is separated from the protocone by a fold or ridge of enamel. This tooth differs further from the succeeding ones in the greater narrowness of its anterior portion, which produces a shortening of the anterior transverse crest, and the posterior is slightly separated from the external wall. The third and fourth premolars differ comparatively little from the corresponding teeth in the European species; the external crescents are not quite so deeply concave, the outer cingulum is somewhat more, and the inner somewhat less developed. The posterior pillar is large and on wear becomes connected with the posterior crest, so that the hinder valley is completely enclosed.

The upper molars are likewise very similar to those of *A. aurelianense*, except that the transverse crests are somewhat straighter and the conules even more reduced. The third molar is much the smallest of the series and differs quite markedly from the corresponding tooth of the European species. The posterior crest is not curved,

but angulate, running inward at a right angle from the external wall and then turning at an obtuse angle towards the hypocone; somewhat external to the latter it sends off a spur which connects with the posterior cingulum. The posterior valley is thus completely enclosed, even before the tooth is worn down. There is, properly speaking, no posterior pillar, its place being taken by a triangular depression, which is enclosed between the hypocone, the spur from the posterior crest already mentioned, and the elevated cingulum.

B. Lower Jaw (Pl. III, Fig. 25). As in the upper series, the incisors diminish from the median to the lateral. Seen from the front, they are much like the upper teeth, but differ from them in having no well-marked internal cingulum and consequently no invagination such as occurs in the European form. The canine is rather small, possibly a sexual character, and follows the incisors with hardly an interval.

The first premolar is smaller, especially transversely, than the corresponding upper tooth and is very simply constructed. It is narrow and compressed, and consists of a low principal cusp (protoconid) with obscurely marked anterior and posterior basal cusps (para- and metaconids). The second premolar differs considerably from that of *A. aurelianense*. The anterior half of the crown is flattened on the outside; the paraconid is less enlarged and is not separated from the protoconid by an external valley. This tooth appears to have neither anterior nor posterior pillars; a strong external cingulum is present on the hinder half but not on the front. The third and fourth premolars do not differ in any important respect from those of the European form; the anterior pillar appears to be fairly well developed, but the posterior is reduced to very small proportions.

The molars also resemble those of the European species; $\overline{m. 1}$ appears to have a small anterior and a still smaller posterior pillar; in the hinder valley is a small accessory tubercle, but this is, no doubt, an individual variation. The second and third molars have no anterior pillars, the metaconid simply extending across the end of the crest which runs inward from the hypoconid. This crest is not continuous with the metaconid, but is separated from it by a shallow groove. I find exactly the same condition of $\overline{m. 2}$ and $\overline{m. 3}$ in an almost unworn specimen of *A. aurelianense* from Sansan, but in the large animals from Steinheim, which have been figured by Fraas (No. 12, Pl. VI, Fig. 2), all the molars, except $\overline{m. 3}$, have small anterior pillars, and the posterior pillar is exceedingly reduced on $\overline{m. 1}$ and absent on $\overline{m. 2}$. In *A. equinum*, $\overline{m. 2}$ has a much reduced posterior pillar and $\overline{m. 3}$ a large heel. All of the lower teeth from $\overline{p. 3}$ to $\overline{m. 3}$ have a strongly marked external cingulum, but none on the inner side of the crown.

The specimen does not enable us to say much with reference to the character of

the skull (Pl. III, Fig. 23). So far as can be judged from the portions preserved, it very much resembles that of the White River *Mesohippus* and displays comparatively little modernization. The face has become somewhat lengthened by the recession of the orbits, but not so much as in the John Day *Miohippus præstans*; the anterior rim is over m. 2, while in *Mesohippus* it is over m. 1. The infraorbital foramen has accompanied this recession, so that its position with reference to the orbit remains the same as before. In this species it is above p. 4, in *Mesohippus* over p. 3. The orbit remains very low down in the face, or rather has descended still lower relatively, owing to the development of large frontal sinuses, while the molars remaining very short crowned give no occasion for elevating the orbits. Consequently, the supraorbital region has a much greater vertical depth than in the White River genus. The orbit is still open behind, but the postorbital process is somewhat longer and more recurved. The supraorbital foramen of *Equus* is, as in the older genus, represented by a deep notch, but the spine is more prominent and nearer to the postorbital process, which appears to be a step towards converting the notch into a foramen. Not enough of the lachrymal is preserved to determine whether a lachrymal pit is present or not. The cranium is much more elevated above the level of the face than in *Mesohippus*, and this results in giving the zygomatic arch a much more abrupt descent downward and forward. The zygomatic process of the squamosal is rather high vertically, but very thin and compressed. The glenoid cavity has the characteristic equine appearance even more decidedly marked than in the more ancient form and its outer portion is raised into quite a prominent tubercle. The postglenoid process is very largely developed and is much longer, heavier and more rugose than in *Equus*. The elevation of the cranium, unaccompanied by a corresponding rise in the position of the orbits, brings about a curious combination of primitive and advanced characters, a combination which may, for the most part, be referred to the elevation of the cranium together with the retention of the primitive brachyodont dentition. The premaxillary region is decidedly more equine than in *Mesohippus*. Corresponding to the increase in the relative dimensions of the incisors, the horizontal portion of the premaxillaries is more largely developed, especially in the vertical direction. The symphysis is quite high and ends above in an obtuse spine, and the ascending ramus makes a more decided angle with the horizontal part. Compared with the premaxillary of the horse, the chief difference to be observed is the rapid descent of the upper margin of the bone at a point above the diastema between the incisors and canine, so that at this point the vertical height is much less than elsewhere. This feature does not occur in either *Equus* or *Mesohippus*. There is no such constriction of the muzzle behind the canine as is seen in the latter genus.

The mandible has a long, stout and rather deep horizontal ramus, which tapers less anteriorly than in the White River form. The symphyseal portion is long and procumbent, quite sharply constricted at the diastema and expanding again to form the semicircular alveolus in which the incisors and canines are inserted. In this portion of the mandible, this species resembles *Mesohippus* more than *Equus*; it differs from both in the rapid rise of the inferior border towards the chin. The ascending ramus is also intermediate in character between the same genera. With the former it agrees in the shape of the angle, which is set off from the posterior border by a notch some distance below the condyle; in the broad anterior border of the ascending ramus, with its deep groove for the buccinator and maxillo-labial muscles and prominent linea obliqua externa. The latter gradually approximates the linea interna and unites with it to form the anterior border of the coronoid. On the other hand, the ascending ramus is decidedly higher than in *Mesohippus* and the condyle is greatly elevated above the level of the molars, in correlation with the raising of the base of the cranium already referred to. This elevation is, however, much less in proportionate amount than occurs in the horse, where the vertical height of the ascending ramus, measured to the condyle, is more than half the length of the horizontal ramus (about 5:8). The coronoid is much better developed than in either the lower Miocene or the recent genus; it is very high, erect and compressed; the free end is somewhat flattened obliquely and recurved, and the posterior border is nearly straight. The coronoid notch is narrower and deeper than in the White River species, and the condyle more extended transversely, especially towards the external side.

Measurements.

	M.
Mandible, length.....	.305
Mandible, height of condyle.....	.126
Mandible, height of coronoid from sigmoid notch.....	.052
Mandible, depth at $\overline{p.1}$030
Mandible, depth at $\overline{m.3}$052
Lower median incisor, width.....	.010
Lower second incisor, width.....	.009
Lower third incisor, width.....	.007
Lower molar-premolar series, length.....	.148
Lower premolar series, length.....	.078
Lower first premolar, length.....	.013
Lower first premolar, width.....	.006
Lower second premolar, length.....	.021
Lower second premolar, width.....	.009
Lower third premolar, length.....	.022
Lower third premolar, width.....	.013

Lower fourth premolar, length.....	.022
Lower fourth premolar, width.....	.014
Lower molar series, length.....	.070
Lower first molar, length.....	.023
Lower first molar, width.....	.014
Lower second molar, length.....	.022
Lower second molar, width.....	.012
Lower third molar, length.....	.025
Lower third molar, width.....	.010
Upper median incisor, width.....	.011
Upper second incisor, width.....	.010
Upper third incisor, width.....	.009
Upper molar-premolar series, length.....	.147
Upper premolar series, length.....	.083
Upper first premolar, length.....	.014
Upper first premolar, width.....	.011
Upper second premolar, length.....	.025
Upper second premolar, width.....	.025
Upper third premolar, length.....	.025
Upper third premolar, width.....	.027
Upper fourth premolar, length.....	.025
Upper fourth premolar, width.....	.026
Upper molar series, length.....	.068
Upper first molar, length.....	.025
Upper first molar, width.....	.028
Upper second molar, length.....	.025
Upper second molar, width.....	.027
Upper third molar, length.....	.021
Upper third molar, width.....	.022

The discrepancy between the measurements of individual teeth and the totals of the molar and premolar series is due to overlapping.

I know of no materials which would render possible a detailed comparison of the skull structure of this species with that of *A. aurelianense*, the European specimens which have been figured being extremely imperfect in this respect. Some points of interest may, however, be determined. In the European species the orbit occupies the same position as in the American, but the infraorbital foramen is slightly farther forward. The zygomatic arch appears to have a less abrupt descent anteriorly and the base of the cranium to be less elevated. The premaxillaries are very different in appearance; the alveolar portion is shallower and the symphysis shorter and devoid of the conical elevation at the top; it is also of more uniform depth and its upper margin does not show the abrupt descent above the diastema which is so characteristic of *A. equinum*. The horizontal ramus of the mandible is deeper and the rise of the inferior margin at the symphyseal portion and the chin

much more decided and abrupt. The ascending ramus appears to be shorter and the condyle is less elevated above the level of the molars.

The Vertebral Column (Pl. II, Figs. 18–20). The atlas is elongate antero-posteriorly in proportion to its transverse width; the anterior cotyli for the occipital condyles are very deeply concave, but somewhat narrow and depressed from above downward. Their lateral anterior margins are notched quite deeply and the inferior portion is flared, so as to present forward instead of upward. Below, the cotyli are separated only by a narrow and shallow groove, but superiorly they are kept wide asunder by a very deep emargination of the neural arch, which is much more pronounced than in *A. aurelianense*, *Mesohippus*, or *Equus*. The neural spine is indicated by a faintly marked ridge and is enclosed in a lyrate area formed by the surface of attachment for the small posterior straight muscles of the head; this area is more distinctly shown than in any other equine which I have examined. The inferior arch is strongly convex and is constricted in the middle to form the deep inferior fossæ; the hypapophysis is prominent and forms a large rugose tubercle. The transverse processes are broken away, but enough remains to show that the atlanteo-diapophysial notch has not been converted into a foramen; this notch is continued backward as a groove into the foramen for the first spinal nerve. The line of attachment of the transverse process pursues a straight course downward and backward and does not describe the slight sigmoid curve which is seen in *Mesohippus*. The foramen of the vertebrarterial canal pierces the process on the dorsal side. The articular surfaces for the axis present less directly backward than in *A. aurelianense*; in shape, these surfaces are triangular, with the long diameter placed vertically; the facets are reflected forward upon the inner walls of the neural canal and are connected below by the broad surface for the inferior face of the odontoid process.

Compared with the atlas of the European species, the chief difference to be observed is the very much greater depth of the notch which separates the dorsal margins of the anterior cotyli.

The axis, so far as it is preserved, closely resembles that of *A. aurelianense*; it has a very much depressed and strongly keeled centrum, which expands anteriorly to give space for the atlanteal facets. The latter are higher and narrower and rise more upon the sides of the neural canal than in the horse. The odontoid process is longer than in the European form and is pointed at the end, as in that species, instead of being truncate, as in the horse. The articular surface on the ventral side of the process is continuous with those on the centrum. The spout-like shape of the odontoid is even better marked than in the existing genus, owing to the greater elevation of the margins. These raised margins do not, however, extend for the full length of

the process, but allow the tip to project freely beyond them, which gives to the ventral aspect of the odontoid a trifid appearance. This feature is more emphasized in the European form than in the American.

Other cervical vertebræ accompany the specimen, but unfortunately they are so badly damaged that little can be learned from them beyond the fact of their strongly opisthocœlous centra and the generally equine nature of their processes.

The posterior thoracic and lumbar vertebræ are likewise opisthocœlous and have long, heavily built centra, with spines compressed and inclining forward; the zygapophyses are quite flat and show the equine character of cylindrical, interlocking processes only in very moderate degree; it is somewhat more distinctly displayed in the lumbar region.

Fore Limb (Pl. II, Figs. 21, 22; Pl. III, Figs. 26-28; Pl. IV, Figs. 30, 31). The humerus is of the same size as that of *A. aurelianense*, but differs from it in many details of construction, in which it approaches the horse more closely than does that species. As in the latter, the head projects much more strongly backward than in the modern type, but resembles the structure of *Equus* more than that of *A. aurelianense* in its greater flatness. The greatest difference, however, between the two species of *Anchitherium*, in regard to the humerus, consists in the character of the tuberosities. According to Kowalevsky, the structure of the proximal end in the European form is intermediate in character between the tapir and the horse; the external tuberosity is almost as large as in the former and the internal is also very similar to what we find in that animal; but in the bicipital groove is a small, rounded eminence, the beginning of the bicipital tubercle which reaches such prominence in *Equus*. In *A. equinum* the tuberosities are more as in the latter genus; the external one is much reduced, but the summit of the anterior portion rises higher than in the recent form, while the crest to which the subspinatus muscle is attached has a greater antero-posterior extent but is less elevated. The outer bicipital groove is much shallower than in the horse and the bicipital tubercle, though broader, is much less prominent and clearly defined. The external and bicipital tuberosities form a broad crest, which rises much higher above the level of the head than in the existing genus and entirely different from the corresponding structure in *A. aurelianense*. The shaft is massive, broad, and flattened proximally, becoming round in the middle and flattening again distally. The deltoid hook and ridge are well developed, though less so than in the horse, and the hook is placed higher up on the shaft than in the European species. The distal end is much more equine in appearance than in the latter, though as in it the trochlea projects more anteriorly than in the horse, which, in connection with the stronger posterior projection of the head, gives to the whole bone a much more

decided sigmoid curvature, when viewed from the side, than in the recent type. The intertrochlear ridge is better developed than in the animals from Sansan and the intertrochlear furrow not so deep; the borders of the anconeal fossa are much more prominent and directed more obliquely towards the inner side and the inner margin is nearly vertical and parallel to the long axis of the shaft, as in the horse. The supinator ridge is less prominent than in the latter. Altogether, the humerus of *A. equinum*, both in its proportions and in the details of its construction, approximates the modern type much more decidedly than does that of the European species.

The ulna is quite different from that of the last-named species, in some respects being more equine and in others less so. The shaft is much reduced, but it is not interrupted and at no point is there any coössification between the ulna and radius, though doubtless this feature is subject to variation, as it is in *Mesohippus*. In order to make clear the differences between the two species of *Anchitherium*, with regard to the structure of the ulna, it will be best to give Kowalevsky's description of it in the French species, which is essentially as follows: The olecranon is much compressed and resembles in general that of the Palæotheria in the absence of that curvature towards the inner side which is characteristic of the horses. As in the latter, the sigmoid facet is not continuous, but is interrupted on the external border by a deep sulcus. The proximal radial facet is continuous, not interrupted in the middle. For the distal 40 mm. of its course the ulna is coössified with the radius, but only slightly so, for among thirty specimens which Kowalevsky examined there was but one in which the distal end of the ulna was still attached to the radius.

In *A. equinum* the olecranon has the inward curvature which is found in the horses, but not in so marked a degree, and the process rises more steeply and projects less decidedly backward; the sigmoid facet is not interrupted upon the external margin and especially in the distal portion the humeral surface is very much larger. The radial facets are of very unequal size, the external being much the larger, and the two are nearly but not quite separated by an emargination of the inferior border. The transverse width of the ulna, measured across the radial facets, is very much greater relatively than in the horse. The radio-ulnar arch is as considerable as in *A. aurelianense*, but distal to this the two bones are in contact throughout their entire length, as, according to Kowalevsky's figure, they are not in the European species. The distal portion of the bone is also very different from what we find in that species; the lower part of the shaft expands into quite a broad plate, which is received into a deep notch in the radius; beneath this, the shaft abruptly contracts, expanding again distally to form the carpal surface. The latter is also different from that of the European form, where it is triangular with its greatest diameter directed transversely,

while in the American species, as in the horse, it is much deeper antero-posteriorly than broad transversely and projects behind the lunar facet of the radius. The external side displays no such tendinal sulcus as in the horse; the pisiform facet is narrower than in that animal but relatively higher.

The radius is, in many respects, more like that of the modern type than is the same bone in *A. aurelianense*, but still retains a number of primitive features. The proximal end is expanded transversely, though somewhat less so than in the horse, a difference which is partly due to the much smaller size of the tuberosity for the attachment of the external lateral humero-radial ligament. The bicipital tuberosity occupies very much the same position as in *Equus*, but is reflected somewhat more upon the internal face and the internal ligamentous process is more prominent. The humeral facets are very similar in the two genera, but the intertrochlear ridge is narrower in the extinct animal, and the deep sulcus which in the horse invades this ridge is, in *A. equinum*, represented by a small raised surface with roughened borders. The intertrochlear furrow is well marked, though less so than in *Equus*, and produces a shallower emargination of the anterior rim. The facet external to this groove is relatively broader than in the modern genus. The shaft is of very uniform dimensions throughout; it is slightly arched forward, broad, and antero-posteriorly compressed, and in general very similar to that of *Equus*, but is more slender and rounded, less expanded and more trihedral distally, where the inner face forms an angle with the anterior, instead of curving gently into it. This trihedral shape is found in all of the primitive equines and even persists in *Desmatippus*. The sulci for the extensor tendons are narrower and have less rugose and elevated margins than in *Equus*. The postero-external angle of the shaft forms, for most of its length, a roughened ridge, to which the ulna is closely applied, and just above the distal end is deeply notched in order to receive the expansion of the ulnar shaft already referred to. Beneath this notch the radius expands to its maximum distal breadth and then narrows again to the carpal surface. The latter is almost exactly as in *E. caballus*, the following being the only differences which can be observed: (1) The scaphoid facet is more concave in front and descends more abruptly behind; (2) the same facet narrows at the posterior projection behind the plane of the lunar surface, instead of being of nearly uniform width; (3) there is no facet for the lunar upon the ulnar side of this scaphoid projection; (4) the lunar facet is not reflected so far upon the posterior side of the bone.

From this description it will at once be evident that the radius of *A. equinum* approximates that of the modern forms very closely, and thus departs considerably from *A. aurelianense*, which displays this modernization in a less degree, as may be

seen from the following points of difference: (1) In the European species the shaft is less broad and flat, more slender and rounded; (2) the bicipital tubercle is on the internal face; (3) the proximal end is less expanded; (4) the distal end is narrower and more distinctly trihedral; (5) the carpal surfaces have less antero-posterior extension, and, in particular, the scaphoid surface extends less behind the plane of the lunar. In this respect, the carpal facets of *A. aurelianense* resemble more those of *Equus asinus*, while *A. equinum* approximates *E. caballus*.

The Carpus (Pl. IV, Fig. 31). The proportions of the scaphoid are very similar to those seen in the horse, it being only slightly narrower and higher in relation to its depth fore and aft. The proximal surface, however, differs from the condition found in the modern genus in a way corresponding to what has already been described in the radius, viz., in the greater convexity of the anterior portion and narrowness in the palmar part. Distally, the differences are more important, as is seen in the much less relative size of the magnum facet and the narrower and more deeply concave surface for the trapezoid, as well as in the presence of a distinct facet for the trapezium, which is absent in the horse. The facets for the lunar are smaller and less projecting than in the latter. The scaphoid of the European species is almost precisely the counterpart of that of the American form; the antero-external angle is somewhat more elevated and the distal facets have a slightly different shape.

The lunar differs from that of *Equus* much more than does the scaphoid; it is both higher and narrower, and the proximal surface especially has smaller proportionate diameters, both transversely and antero-posteriorly. The radial facet differs in being quadrate rather than triangular; it is much less extended on the palmar side and lacks the additional facet on the posterior crest which occurs in the recent animal; in front, the descent towards the radial side is both greater and more abrupt; the lateral facets for the scaphoid and cuneiform are much less prominent, and hence the median constriction of the lunar, when viewed from the front, is not nearly so marked. Distally, we note that the unciform facet is wider and more oblique and that for the magnum is smaller in both dimensions; this is especially true of its posterior prolongation, the well-developed, knob-like process projecting considerably beyond it, as it does not in the horse. The lunar of the European species differs from that of the American principally in the greater breadth of the facet for the unciform and the less antero-posterior extent of that for the magnum.

The cuneiform has a much greater antero-posterior, as compared with its vertical diameter, than is the case in the horse; it is also narrower transversely and more compressed. The principal pisiform facet is much smaller and is not isolated, as in *Equus*, but is connected with the ulnar facet by a narrow articular surface. The

distal facet for the unciform is more deeply concave in front. Kowalevsky does not figure this bone in the French specimens.

The pisiform is very different in shape from that of *Equus caballus* and is more like that of *E. burchelli*. Compared with the pisiform of the former species, it is very less broadened vertically, is more recurved at the free end, and there is a greater difference in vertical diameter between the proximal and distal ends. The principal cuneiform facet is sessile, not strongly projecting, and is connected by a narrow band with the upper facet. In *A. aurelianense* this connection is not found, and the cuneiform facet is very prominent, as in *Equus*, but, on the other hand, the free portion is even more slender and tapering than in the American species.

The trapezium is not preserved in the specimen, but its presence is demonstrated by the facets upon the scaphoid, trapezoid and second metacarpal.

The trapezoid is likewise very equine in character, but with some not unimportant differences of detail. The facet for the scaphoid is somewhat less strongly convex and continues posteriorly, without interruption, into the small surface for the trapezium. Distally, the divergences between the two genera are more marked. In *Equus*, behind the large surface for the second metacarpal, there is a facet for the posterior part of the head of mc. iii, and, at right angles with this, a surface for the magnum, the two together forming a conspicuous projection. In *A. equinum*, on the other hand, the trapezoid has no contact with mc. iii, and the posterior contact with the magnum is very limited and appears not to form a facet. In this species, also, the trapezoid is less completely concealed by the magnum when the carpus is seen from the front. On the ulnar side there are two well-developed facets for the magnum, which are separated by a narrower interval than in the horse. The trapezoid of the European species is unknown, but the facets on the adjoining bones show that it was very much as in the American form.

The magnum is, in general, extremely equine, but differs in many minor points from that of existing species. It is higher and narrower in the fossil; the proportions of the two proximal facets are about as in the horse, except that the posterior convexity, or head, is very much narrower. As in the existing species, this head is covered entirely by the lunar and has no contact with the scaphoid. On the radial side of the magnum are two facets for the trapezoid and a small oblique surface for mc. ii; the posterior trapezoid facet, which is so conspicuous in *Equus*, does not occur. On the ulnar side, the unciform facets are quite different from those of the horse. In the latter genus the two anterior unciform surfaces are close together and sometimes confluent, and the posterior facet occupies more than half the vertical diameter of the head. In *A. equinum* all three facets have a much smaller vertical

extent and the two in front are widely separated; the superior one is narrower but extends much farther back upon the side of the head. On the distal surface several notable differences are to be observed. In the fossil, the anterior border describes a decidedly smaller arc of a circle and the middle line of the posterior prolongation is nearly coincident with the middle line of the bone, while in the horse the radial portion of the magnum has been much extended, which gives to the hinder prolongation a more unsymmetrical position; it is also very much broader and its hinder margin straighter and more oblique in direction, and forming angles with the lateral borders, instead of being connected with them by curves as in *A. equinum*. The magnum of *A. aurelianense* is altogether like that of the American species, except for the confluence of the two anterior unciform facets.

The unciform has, unfortunately, been lost from the manus of both sides, but there is no reason to doubt its resemblance to that of the European species in all important respects.

The Metacarpus. The second metacarpal has a head of more primitive form than in *Equus*; it is less extended antero-posteriorly in proportion to its breadth, and not only rises above the head of mc. iii, but slightly overlaps it, in order to reach the magnum. The two facets for mc. iii are distinctly, though not so widely, separated and the anterior facet is plane, not concave. As the head of mc. iii has a much smaller extension towards the radial side, mc. ii is less crowded backward and is more completely visible from the front. The surface for the trapezoid is less flattened, but remains slightly concave, and passes on the palmar side into a small facet for the trapezium, which is lost in the modern genus. The shaft is long, very much compressed laterally, but retaining a considerable antero-posterior depth; the same is true of the distal end, which measures almost as much from before backward as does the distal trochlea of the median metacarpal. The carina is but feebly developed and entirely confined to the palmar side of the trochlea. In the specimens of *A. aurelianense* from Sansan, which Kowalevsky has figured, mc. ii differs from that of *A. equinum* only in the following particulars: The proximal portion is triangular, not irregularly quadrate in shape; the facet for mc. iii is not divided into two parts; and the distal trochlea is more recurved. Fraas has, however, figured a specimen from Steinheim (No. 16, Pl. VI, Fig. 12) in which the lateral metacarpals are of proportionately enormous dorso-palmar extent, far more so than in the American form.

The third metacarpal differs in many important respects from that of *Equus*; the proximal end is much less expanded transversely, while its depth from before backward remains relatively less. Owing to this less expansion transversely, the

anterior facet for mc. ii presents more laterally and less posteriorly. The unciform facet is single, but the deep sulcus, which in *Equus* divides it into two parts, is present in an incipient stage; this facet is still entirely lateral and but little oblique in position, while in the horse it has become altogether proximal. The facet for mc. ii is double, but that for mc. iv still remains single, though showing a tendency to divide into two parts. A striking difference between the two genera in regard to the head of the median metacarpal lies in the very much narrower posterior portion in the fossil. In the horse this region is extended beneath the unciform, on the one hand, and the trapezoid on the other, and is separated, on the ulnar side, by a deep sulcus from the anterior portion of the magnum facet. In *A. equinum* this posterior region does not touch the trapezoid, its contact with the unciform is lateral, and the sulcus which invades the magnum facet is only incipient. The shaft is of very uniform dimensions, contracting very little below the head, where it is of transversely oval section; for most of its length it retains much the same form and size, but towards the distal end it gradually widens and becomes more flattened. The distal trochlea is low and narrower than the shaft, which is broadened just above the trochlea by the tubercles for the attachment of the lateral ligaments. The carina is prominent upon the posterior surface but dies away upon the anterior. In *A. aurelianense* the specimens differ considerably in the character of the median metacarpal. In those from Sansan the bone is very much as in the American species, but the facet for mc. iv is double and the distal keel extends farther upon the anterior face. In the specimens from Steinheim the keel is entirely restricted to the palmar side, but the proximal end is quite modernized by the rounding of the anterior border of the magnum surface, the widening of the posterior extension of this facet, and the partial separation of the two by a sulcus from the ulnar side.

The fourth metacarpal has a narrow, slightly concave head for the unciform, and the posterior side displays a small facet for the proximal end of the rudimentary mc. v. The shaft is truncated obliquely for about an inch below the head and forms a roughened surface, to which the styliform rudiment was no doubt closely applied. The shaft and distal end of mc. iv are the counterparts of mc. ii. A rudiment of mc. v was also present in the European species.

The Phalanges (Pl. III, Figs. 27, 28; Pl. IV, Fig. 31). In the lateral digits the phalanges are different in many details from those of the French specimens of *A. aurelianense*. The proximal phalanx is shorter in proportion to that of the median digit, though of the same actual size, and relatively to the length of the metacarpals; beneath the proximal thickening the bone is more suddenly constricted and then thickens again slightly to form the distal trochlea. The lateral profile is thus very

different from that of the French specimens and, seen from the front, it is much straighter and less arched outward than in Kowalevsky's figure. Gaudry, however, represents it more as in the American species (No. 13, Fig. 176). I may add here that the latter drawing shows a very much wider median metacarpal than in *A. equinum*, broader in proportion to its length than in *Protohippus* or *Hipparion*.

The second phalanx differs from that of the European species, especially in the very much greater development of the posterior "salient beak," which is formed by a prolongation of the external half of the proximal surface. This, together with the more marked median constriction, gives the side view of the second phalanx quite a different appearance in the two species.

The lateral unguals are still more different. In the Sansan specimens of *A. aurelianense* "this phalanx is very small; it has the shape of a right-angled triangle, of which the hypotenuse forms the postero-inferior border and the right angle is placed antero-superiorly. . . . It does not differ appreciably from the same phalanx of *Hipparion*" (Kowalevsky, p. 69). In *A. equinum* the ungual is much larger in every dimension, especially in the length of the postero-inferior border; the so-called "basilar process" and "wing" are also better developed, and the outline is that of a spherical triangle, all of the borders being curved. In length this bone much exceeds either of the other phalanges and must have had distinctly more functional importance than in the typical forms of the European species. Fraas' figure of the lateral ungual from Steinheim shows a phalanx which is again different from both the French and American forms, though considerably nearer to the latter, as is shown by its elongation and extended "basilar process."

The phalanges of the median digit are likewise somewhat different from those of *A. aurelianense*. Kowalevsky's account of their form in this species has already been quoted in the description of *Desmatippus* and it is unnecessary to repeat it here. The dimensions of the proximal phalanx in *A. equinum* agree very well with the largest specimens of the French species from Sansan, as given by Kowalevsky, except for the greater antero-posterior depth of the proximal end. The groove for the carina of the metacarpal is less profound and not continued so far forward; the triangular roughened surface for the attachment of the sesamoid ligaments is somewhat more prolonged towards the distal end. The intercondylar notch which emarginates the distal trochlea on its palmar edge is much less conspicuous than in the European species or the modern horse.

The second phalanx is not preserved in the specimen.

The ungual phalanx is unmistakably equine in character and yet very different from the modern type. It also differs strongly from the usual form of ungual which

occurs in *A. aurelianense*, though the latter species displays a considerable degree of variation in this regard. In the specimen figured by Kowalevsky the ungual is very long, depressed, and pointed towards the distal end, and yet with considerable dorso-palmar depth. Gaudry's figure of the same species exhibits a decidedly more modernized hoof, marked by the more rounded border of the palmar surface, the greater vertical depth and consequent steeper inclination of the anterior face; the proximal articular facet is much more nearly parallel to the plane of the palmar surface. A third type of ungual which has been referred to this species is shown in Fraas' figures of the large animal from Steinheim. Here the anterior border of the palmar surface is more regularly rounded than in Kowalevsky's specimens, except for the more conspicuously marked emargination in the median line and the groove which runs proximally up the median line of the anterior face of the bone from this emargination. The phalanx is narrower in proportion to its length and the facet for the second phalanx is very steeply inclined to the plane of the palmar surface than in either of the French types, and apparently the bone is more depressed than in the latter. Part of the difference between Kowalevsky's and Gaudry's figures may be due to the fact that the former is of the hind foot and the latter of the fore foot, but this assumption would not account for the Steinheim type, which is different from both.

The ungual phalanx of *A. equinum* is decidedly more like the Steinheim type than either of the French ones, and differs from it principally in the better development of the "basilar processes" and "wings" and in the less deep lateral constrictions of the bone below the proximal head.

Hind Limb. The pelvis is very like that of *Mesohippus*, except in size, and approximates the modern type but little more than does that of the White River genus. As compared with the pelvis of the horse, the neck or shaft of the ilium is much longer, the plate less expanded and everted, and the gluteal surface less concave; the pit for the origin of the rectus femoris muscle is smaller, deeper, and much nearer to the acetabulum. The iliac surface is rather narrower and the pubic border less prominent than in *Mesohippus*. The acetabulum has prominent margins and the sulcus for the round ligament is less extensive and narrows the articular surface less than in *Equus*; it has the peculiarity that the end of the sulcus, where the anterior and posterior borders meet, is angulate instead of curved. The ischium is straighter and more slender, the obturator foramen very much larger and more oval, and the descending plate of the ischium much less expanded than in the modern form. The supra-acetabular crest is but feebly developed and the tendinal sulci not deeply cut. The pubis is likewise more slender and less rugose than in *Equus*. Little is known of the pelvis in *A. aurelianense*, but the fragments preserved show an important dif-

ference from the American species in the ischiadic or supra-acetabular crest, which is more rounded and thickened even than in the horses. Both species agree in having a sulcus for the tendon of the internal obturator muscle.

The only other part of the hind limb of *A. equinum* which is known consists of some fragments of the distal ends of the metatarsals and phalanges of another specimen. These are larger than the corresponding parts of the manus, but otherwise like them.

The type specimen of *A. equinum* was found by Mr. I. Benet in the upper beds of Deep river (lower Loup Fork), Mont.

Measurements.

	A. EQUINUM.	A. AURELIANENSE.
	M.	M.
Humerus, length.....	.224	.230
Humerus, width of proximal end.....	.066	.063
Humerus, depth of proximal end.....	.072	.075
Humerus, width of distal trochlea.....	.053	.049
Radius, length.....	.265	.250
Radius, width of humeral trochlea.....	.051	.050
Radius, width between inferior tuberosities.....	.050	.060
Radius, width of shaft in the middle.....030
Radius, depth of shaft in the middle.....019
Radius, depth of humeral surface.....	.026	.025
Radius, width of facets for the ulna.....	.031	.040
Scaphoid, width of proximal end.....	.019	.017
Scaphoid, width at middle.....	.016	.014
Scaphoid, width of distal end.....	.018	.015
Scaphoid, height of anterior face.....	.021	.023
Lunar, width of distal end.....	.018	.017
Lunar, width of unciform facet.....	.007	.005
Lunar, height of anterior face.....	.022
Cuneiform, height.....	.016
Cuneiform, depth of distal end.....	.023
Trapezoid, height.....	.012
Trapezoid, width.....	.011
Magnum, anterior height.....	.015	.013
Magnum, anterior width.....	.030	.025
Magnum, posterior width.....	.010	.007
Magnum, posterior height.....	.018	.021
Magnum, depth.....	.026	.026
Pisiform, length.....	.033
Pisiform, height of proximal end.....	.011
Metacarpal iii, length.....	.194	.196
Metacarpal iii, width of proximal end.....	.028	.030
Metacarpal iii, width in the middle.....	.023	.024
Metacarpal iii, width of distal end.....	.028	.023

	A. EQUINUM.	A. AURELIANENSE.
	M.	M.
Metacarpal iii, depth of proximal end.....	.023	.024
Metacarpal ii, length.....	.179
Metacarpal ii, width of proximal end.....	.010	.008
Metacarpal ii, depth of proximal end.....	.014	.013
Metacarpal ii, width of distal end.....	.011
Metacarpal ii, depth of distal end.....	.020
Metacarpal iv, length.....	.177
Metacarpal iv, width of proximal end.....	.011
Metacarpal iv, depth of proximal end.....	.014
Metacarpal iv, width of distal end.....	.012
Metacarpal iv, depth of distal end.....	.020
First phalanx of median digit, length.....	.040	.040
First phalanx of median digit, width of proximal end.....	.033
First phalanx of median digit, width of middle.....	.027	.028
First phalanx of median digit, width of distal end.....	.026	.027
Third phalanx of median digit, length.....	.043	.041
Third phalanx of median digit, width of proximal end.....	.033	.0285
Third phalanx of median digit, maximum width.....	.046	.044
First phalanx of lateral digit, length.....	.026	.027
Second phalanx of lateral digit, length.....	.015	.016
Third phalanx of lateral digit, length (plantar border).....	.042	.028

The Systematic Position of Anchitherium.

The relation of *Anchitherium* to the other genera of the equine phylum is a problem of more than ordinary interest, for if we can once establish its systematic position with reasonable probability, we shall find that the inferences which may be drawn from the facts have a very important bearing upon many of the open questions as to the mode in which transformation may operate in a given case. The European palæontologists have very generally regarded this genus as ancestral to the modern *Equidæ*, and many of these authorities have derived *Anchitherium* from *Palæotherium*, *Paloplotherium*, or some similar type. Had the wonderful series of American equines never been discovered, it is highly probable that this result would not have been disturbed, though in the light of present knowledge it cannot be accepted. It is not worth while to argue against the derivation of *Anchitherium* from *Palæotherium* or an allied genus, for since Marsh directed attention to the equine nature of the Eocene *Hyracotherium* and its allies, the older hypothesis has been almost entirely abandoned, but the position of the genus before us with reference to the existing *Equidæ* and to preceding genera is a much more difficult and obscure problem, more especially since it involves the supposed dual origin and parallel lines of horses in the Old World and the New.

The facts which exploration is continually bringing to light tend more and more strongly to the confirmation of Schlosser's view. "Derselbe [d. h. der Pferdestamm] hat schon frühzeitig Representanten in Europa sowohl als auch in Nordamerika, doch sind nur die neuweltlichen Glieder dieses Stammes von wesentlicher Bedeutung, indem die altweltlichen sämtlich früher oder später ohne Hinterlassung von Nachkommen wieder ausgestorben sind. Die europäische Reihe ergänzte sich immer wieder durch Einwanderung amerikanischer Typen. Erst vom Pliocän an scheint der Pferdestamm in der alten Welt weiter entwicklungsfähig geworden zu sein" (No. 30, p. 486).^{*} That the genus *Anchitherium* itself, even in the restricted sense in which I have used that term, is of American rather than European origin is rendered probable by the following considerations: (1) In the Old World the equine series is very fragmentary and incomplete; between *Pachynolophus* of the upper Eocene and *Anchitherium* of the upper Miocene there is a great gap, which no known European genus tends to bridge over, for assuredly *Anchilophus* cannot be considered in this connection. The three descending stages in the phylum, which we call *Epihippus*, *Mesohippus* and *Miohippus*, have as yet yielded no representatives at all in Europe, and even should one or other of them be found there hereafter, it is not in the least likely that such a wealth of individuals and species as characterizes the various horizons of the upper Eocene and the Miocene in this country will be discovered in the Old World. That the line should be thus broken in the Eastern and uninterrupted in the Western Hemisphere is surely a strong indication that the latter was the theatre of its development, especially in view of the abundance of both individuals and species. (2) There is little difficulty in deriving *Anchitherium* from some of the species of *Miohippus*; the changes involved are slight, though some of them are of much morphological significance. (a) In the first place, there is great increase in size, both of the known species of this genus much exceeding any known form of *Miohippus*. (b) In the upper molars and premolars the conules are reduced in relative importance and the posterior transverse crest has become connected with the outer wall of the crown. (c) In the lower premolars the internal cusps (*a*, *a'*, *b*, *b'*, of Rüttimeyer) are likewise reduced, and in more or fewer of these teeth the pillars, anterior and posterior, are obsolete. A similar tendency may be observed in some forms of *Miohippus*. (d) The odontoid process, which in the John Day genus is just beginning to assume the spout-like shape, has in *Anchitherium* become as completely so as in the horse. (e) The median digit of both manus and pes has become greatly enlarged and thickened, though there is no great reduction of the lateral digits, and

^{*}I believe Mme. Pavlow has expressed a similar opinion as to the position of *Anchitherium*, though I cannot lay my hand upon the reference.

in the Steinheim specimens they seem even to be enlarged. (*f*) The median ungual phalanges are much elongated, but in most forms of the genus they are much depressed and flattened and have gained but little in vertical diameter.

Some of the species of *Miohippus* already point in the direction of *Anchitherium*, as we have seen to be the case in regard to the inner cusps of the lower teeth. The typical form of ungual phalanx in the John Day genus is that of *M. anceps* as figured by Marsh (No. 27), in which that of the middle digit is relatively short and differs but little from the hoof of *Mesohippus*, but in a specimen obtained by the Princeton party of 1889 on the Middle Fork of the John Day river, in eastern Oregon, this phalanx is very much elongated, depressed and narrowed, so as to recall in a striking manner the corresponding bone of *Anchitherium* (see Pl. II, Fig. 16). As this specimen is not accompanied by teeth, I cannot yet refer it to any described species of *Miohippus*, but that, in one respect at least, this species tends strongly towards *Anchitherium* is obvious. There remains, however, one point as to which there is much uncertainty. In *A. aurelianense* the meso- and ectocuneiforms are coössified, while in all other equines in which the tarsus is known the external cuneiform is free and the median united with the internal. Kowalevsky does not state how many specimens he was able to examine, and thus to determine whether the condition which he describes in the French forms is the invariable rule or only an occasional variation, such as Forsyth Major has shown to occur not very infrequently among recent horses (No. 15, p. 63). Unfortunately, nothing is known as to the condition of the tarsus, in this respect, of the specimens from Steinheim and of *A. equinum*.

Until the question is determined as to whether the coalescence of the meso- and ectocuneiforms be the normal condition in *Anchitherium*, it is useless to speculate on the way in which this peculiarity was brought about, but a hint of the possible method is given by the specimens shown in Pl. II, Fig. 15, which is of a White River *Mesohippus*. In this animal all three cuneiforms have coalesced into a single piece, which may possibly have been the first step, to be followed later by a separation of the internal element. That this particular case is perhaps pathological, is indicated by the ankylosis of the second and third metatarsals, or it may be due merely to age, as there are no exostoses in the joint. Nevertheless, the specimen is not without suggestive value, and the example of the recent horses shows us that such changes may and do take place in the individual. Another indication that variations looking to *Anchitherium* were commenced as early as the genus *Mesohippus*, is afforded by the curious species of that genus, *M. (Anchitherium) cuneatus* Cope, to which Prof. Cope has called my attention. This species displays a strong tendency to assume the concave and inwardly projecting external crescents of the

upper teeth, which are so characteristic of *Anchitherium* and which have, perhaps, as much as any other feature, led to the view of its derivation from *Palæotherium*. (3) *Anchitherium* has now been found in America in strata which are probably as old as, if not older than, those of Sansan and Steinheim, and there is thus no geographical or geological objection to assuming that the two species of this genus have both been derived from some species of *Miohippus* as yet not identified. We may hope to learn much upon this subject when the various species of the John Day genus have been more fully described and their variations in tooth and foot structure correlated.

So far as the relations of *Anchitherium* to later genera of the equine series are concerned, I think the evidence now available strongly confirms Schlosser's view, already quoted, that this genus is an abortive side branch of the main phylum, which died out, leaving no successors behind it. (1) The teeth of *Anchitherium* are in some important respects less characteristically horse-like than those of the more ancient genera, as may be seen from the following facts. (a) In the lower molars and premolars of the *Equidæ* no feature is more characteristic than the two pairs of internal cusps (a a¹, b b¹), which originated at a very early period and steadily increase in size and importance until they reach their maximum development in the modern forms. Now, in *Anchitherium*, these elements are reduced in prominence; on some teeth they are missing, and, as in the case of disappearing structures generally, they are very variable. Thus, in the case of the large *A. aurelianense* from Steinheim, figured by Fraas, the anterior pillar is absent on $\overline{\text{m. 3}}$, present on the others; the posterior pillar is much reduced on $\overline{\text{m. 1}}$, absent on $\overline{\text{m. 2}}$. Kowalevsky's specimens are too advanced in wear to show these features, but in a lower jaw from Sansan containing $\overline{\text{m. 2}}$ and $\overline{\text{m. 3}}$, which the Princeton museum owes to the kindness of Prof. Gaudry, the anterior pillar is not found in the last or the penultimate molar, and $\overline{\text{m. 2}}$ has no posterior pillar. The same description will apply to *A. equinum*. In this connection it is important to note that in the milk molars of *A. aurelianense* these pillars are much more conspicuously developed than in the permanent teeth (see Kowalevsky, Pl. III, Fig. 58). (b) In the upper cheek-teeth the posterior conule retains its importance throughout the equine series, and yet in *Anchitherium* it is so much reduced as to be hardly recognizable. (c) The external cusps of the superior molars and premolars in *Mesohippus*, *Miohippus*, *Desmatippus*, *Protohippus* and *Equus* are but slightly concave and do not project inward in any marked degree, while in *Anchitherium* these cusps are more decidedly concave than in any of the earlier or later genera, and their apices project inward in a way that recalls the molars of the titanotheres. All of these features tend to indicate that the dentition

of *Anchitherium* had entered upon a course of development which was not in the direction of the typical horses, but leading away from them, and that in consequence the genus had no place in the direct line.

(2) If we may assume that the coalescence of the meso- and ectocuneiforms in the tarsus is really characteristic of the genus, we shall have a further reason for denying *Anchitherium* a place in the direct ancestry of the horses, for it seems unlikely that the modern condition should have been already attained in *Mesohippus*, lost in *Anchitherium*, and reacquired by the subsequent genera. But, in view of the uncertainty as to the typical character of this structure, we cannot insist strongly upon it.

(3) The very curiously elongated and flattened hoofs of this genus also militate against the view that it belongs in the direct line, since in the change of *Miohippus* to *Desmatippus* they do not represent one of the stages of the transition which we should expect to find.

(4) The very large size of both the known species of *Anchitherium*, one European and the other American, would seem to indicate that this is characteristic of the genus. This size much exceeds that of the forms which, on the hypothesis that *Anchitherium* belongs in the main series, must be regarded as its successors, and such alternations in bulk are unlikely.

(5) There is no vacancy in the direct equine phylum which *Anchitherium* can fill, as the change from *Miohippus* to this genus, though of a different kind, is hardly less in amount than that from *Miohippus* to *Desmatippus*, and to insert *Anchitherium* in the series would be to assume a view of zigzag development, which, as to amount, is unnecessary and unwarranted. As we shall see later, a certain degree of such alternating advance and retrogression very probably does take place, but not to such an extent as this hypothesis would involve. It might be thought that the occurrence of *Anchitherium* in the same horizon with the more modernized genera, *Protohippus* and *Desmatippus*, would be a further argument for excluding the first-named genus from the phylogeny. This fact must, of course, be allowed some weight; but as it is, perhaps, a case of the survival of an older form, just as *Desmatippus* very probably is, no great importance can be attached to it. Such cases must usually be decided upon morphological grounds.

If the view as to the systematic position of *Anchitherium* here contended for be correct, it follows that those features in which this genus approximates the modern forms more closely than does *Miohippus* are phenomena of parallelism. As such, these structures deserve careful attention. Assuming the possibility of parallel development, we might on *à priori* grounds lay down the general principle that the

more nearly allied any two organisms are, the more likely will they be to independently acquire similar modifications. For development is the resultant or outcome of the interaction of two great groups of factors, viz., the nature of the organism and the character of the environment, and obviously the more nearly alike these two classes of factors are, the greater the similarity to be expected in the result. To use Darwin's words: "The members of the same class, although only distantly allied, have inherited so much in common in their constitution that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs strikingly like each other, independently of their direct inheritance from a common progenitor."* Thus there are certain characters which have repeatedly arisen in the artiodactyls, but are not known outside of that group. An example of this is given by the teeth; I have elsewhere shown that the selenodont molar has been, in all probability, independently acquired by at least three very distinct phyla, not including others in which the molar pattern is slightly aberrant from the typical four crescent plan, but outside of the suborder no tooth is known which presents more than a superficial resemblance to this pattern. That this is not, however, the limit of the process, is shown by the spout-shaped odontoid process of the axis in many ungulates, the bicipital tubercle and double bicipital groove of the humerus in the horse and camel, and the numerous resemblances between artiodactyls and perissodactyls which have not been inherited from their common ancestors, the Condylarthra. Indeed we are as yet very far from being able to set a limit to the possibilities of this mode of development, not to mention at all the phenomena of convergence. What is here contended for is the principle (at first sight the most obvious truism) that numerous and close resemblances of structure are *prima facie* evidence of relationship, even though many of these resemblances be due to parallelism, and further, that such parallelisms, when properly understood, may be of great value in morphological and phylogenetic speculation. Even when we exclude *Anchitherium* (and very probably the same reasoning will apply to *Hipparion*) from the direct line of equine descent, we find that most of the conclusions as to the steps of modification in this line which were deduced from the older hypothesis (except, of course, so much of it as referred to the relationships of *Palæotherium*) are still valid and need to be revised only in comparatively few details. Should it prove to be the case that *A. aurelianense* and *A. equinum* have no nearer connection than through some species of *Miohippus*, which was ancestral to

*My attention was called to this passage by its quotation in Prof. H. T. Fernald's paper on "The Relationships of Arthropods" (Baltimore, 1890), which the author has kindly sent me. I have been much interested to see how well Fernald's results in Arthropods agree with my own in mammals.

both, this would not diminish the value of either for understanding the systematic position of the other, but would rather enhance it, for this would render more intelligible the fact that, on comparing the two species, we find now one and now the other more closely approximating the modern standard, and again, both agreeing in some advance beyond *Miohippus*, either towards or away from the modern horses.

As examples of these parallelisms, the following may be selected. (1) In the upper cheek-teeth of *Miohippus* the posterior transverse crests are separated from the external wall, while in *Anchitherium* they have become coalesced with it. This also happens in the direct line, beginning with *Desmatippus*. (2) In the upper incisors the pit or "mark" is much better developed than in the John Day form. (3) The orbit has been shifted farther back than in most of the species of *Miohippus*, though not so far as in *M. præstans*. (4) The size of the animal has greatly increased, and the changes which accompany augmented size and weight, such as heavier limb bones with better developed processes for muscular and ligamentous attachments, are well shown. (5) In *Miohippus* the spout-like shape of the odontoid process of the axis is but barely indicated by a slight elevation of its lateral margins, while in *Anchitherium* this character is much more pronounced and is even carried somewhat farther than in the horse. (6) The median digit in both manus and pes is enlarged, and in consequence the magnum in the carpus and the ectocuneiform in the tarsus have become relatively broader and lower. In these respects the two species agree, in others they differ as to the degree of approximation to the modern standard.

In the following respects *A. equinum* is more modernized than *A. aurelianense*. (1) The base of the cranium is more elevated above the plane of the molar teeth, and this brings about an increase in height of the ascending ramus of the mandible and the mandibular condyle is raised higher. (2) The humerus is much more equine in structure, the external tuberosity being reduced in size, the bicipital tubercle much enlarged, median in position and dividing the bicipital groove into two parts; the distal end also is almost completely like that of the horse in construction. (3) The radius is more equine in the expansion of the extremities, widening and flattening of the shaft, the shape of the carpal facets, and in the position of the tubercle for the insertion of the biceps muscle. (4) The olecranon of the ulna has the inward curvature characteristic of the recent horses; the distal facet for the cuneiform is also more as in *Equus*.

On the other hand, the European species approaches the recent type in several points of structure more nearly than does the American. (1) The lower incisors have the pit or enamel invagination as well marked as the upper. The exact significance of this difference between the two species is not quite clear; it may imply that

A. equinum has lost the structure in question, as is the case with certain horses from the Pliocene of Florida, to which Cope has called attention, or, as is more probably true, the American species never acquired the character. Prof. Cope very kindly allowed me to examine his beautiful series of specimens of *Miohippus* from the John Day beds of Oregon, and in all of them I found that, while the invagination was fairly well marked in the upper incisors, it was not indicated at all in the lower. (2) The sigmoid facet of the ulna is not continuous, but interrupted on the external side by a deep sulcus. (3) The facets on the pisiform for the cuneiform and ulna, respectively, are widely separated. (4) In the specimens from Sansan (but not those from Steinheim, which perhaps should be referred to a different species) the median ungual phalanges are less depressed and flattened and those of the lateral digits are decidedly more reduced in size than those of the American species. (5) The keel on the distal trochlea of the median metacarpal, and the corresponding groove on the proximal phalanx, are more extended anteriorly. This appears not to be true of the specimens from Steinheim, and doubtless, as Kowalevsky has suggested in the case of *Hipparion*, the shortening of the lateral digits is causally connected with the increased size and importance of the metapodial keels.

The evidence here brought forward seems to lead us to the following conclusions. The genus *Anchitherium*, in the restricted sense of the term, is of American origin and reached Europe by migration. It cannot be regarded as a member of the direct ancestry of the modern *Equidae*, but as a side branch of that stem, which was probably derived from some of the John Day forms not as yet identified. Though appearing later in time than these forms, it nevertheless is in some respects more widely removed from the recent horses than they. This is notably the case in the dentition, where the "pillars," and especially the anterior ones, of the lower molars and premolars, and the posterior conule of the upper, appear to be undergoing a retrogressive metamorphosis. Further, in no species of *Miohippus*, or even of *Mesohippus*, are the lateral metapodials so large as in the Steinheim form of *A. aurelianense*. Some of the John Day species have a distinctly more modernized type of skull than any species of *Anchitherium*. In *M. præstans*, for example, the orbit is very far back, shifted almost entirely behind the line of the molars. While the skull of *A. equinum* has great vertical depth in the orbital region, the orbit remains very low in the face and the zygomatic arch descends very abruptly in its passage forward. Though we have still, it is obvious, much to learn as to the exact relationship between *Anchitherium* and *Miohippus*, the general position of the former with reference to the main equine stem is now reasonably clear.

Taking now a broader view of the series of equine genera which have been

described in the preceding pages, we find that it is fitted to throw very welcome light upon some disputed questions of evolutionary philosophy. In a former paper (No. 33, p. 371) I considered the problem as to whether the differentiation of any group is a steadily advancing one (or retrograding, as the case may be), interrupted only by relatively stationary periods of rest, or whether it should rather be regarded as progressing in a spiral, advancing, on the whole and in the long run, but with many deviations, setbacks and retrogressions. The evidence then available from fossil mammals did not seem to give any very definite answer to this question, and, while the new material offers important help in the solution of the problem, we cannot hope to solve it definitely. The grand difficulty in the way of applying the results drawn from the study of mammalian phyla to the solution of such general questions lies in the fact that only very rarely can we construct a phylogeny of species as distinguished from that of genera, and the latter are too vague for the purpose. A hardly less formidable difficulty is caused by the influence of migrations from one region to another. The phenomena of parallelism, interesting as they are in themselves, are often impossible to distinguish from the effects of a common inheritance, and the tendency in successive genera to repeat similar cycles of specific variation only adds to the confusion. Sometimes an apparently simple and easy step in advance is delayed for an incredibly long period. Thus in the little *Mesohippus* the ulna is as much reduced and as frequently coössified with the radius as in the very much larger *Anchitherium* which appears so much later in time. The lachrymal pit is constant until we reach *Miohippus*, when it becomes subject to variation, one species at least being devoid of it, while in the much more advanced genera, *Protohippus* and *Hipparion*, the same variation is found, some species having the pit and others not. Yet a phylogenetic scheme founded upon the presence or absence of the lachrymal depression would lead to absurd results. Still another obstacle to progress in these questions is found in the conditions of preservation of the fossils. As we examine large series of forms from several successive horizons, we find that the great majority of species and genera are confined to one or two formations and that each succeeding fauna is recruited partly by migration from other regions, partly by the rapid expansion of a comparatively few adaptive and plastic types, while most of the forms which were especially fitted for the older conditions die out under the new. Now, the collections contain, principally, the dominant and abundant species of any given horizon, and these are frequently not the ancestors of the species which will be dominant in the succeeding period. Only rarely do we find so many lines keeping on without break from one horizon into another as those which pass from the White

River up into the John Day. Hence the exceptional value of those two formations for the study of phylogenetic problems.

Admitting the full weight of the difficulties above mentioned, some general principles stand out clearly from the confusion. The clearness may be deceptive, but that must be determined by wider investigation. In comparing the series of horse-like genera, we are struck at once by two facts: first, the steady advance of differentiation in the main, and, secondly, the continually alternating progress and regression in certain minor details. Every genus is in some respect or other, often very trivial, less modernized than its predecessor. For example, we have seen that, in certain details of the carpus and tarsus, *Mesohippus* is more advanced than *Miohippus*, *Miohippus* more than *Desmatippus*, and the latter again than *Protohippus*. It is worthy of note that not always the same structures are affected by the retrogression in the various genera; we do not find continual advance in some respects balanced by continual retreat in others. On the contrary, each genus would appear to recover part, at least, of the ground lost by its predecessor, but to lose in some other direction itself. Part of this appearance of alternation is no doubt due to individual variation, for a character is often long subject to great variation before becoming finally established, and, as already stated, there is in each successive genus a tendency to run through similar cycles of variation. No doubt, also, allowance must be made for the difficulty of constructing a phyletic series of species, so that, if these appearances were confined to the horses, no great weight could be attached to them, but every phylum which I have been able to carefully examine displays the same phenomena. In view of the very close connection between the John Day and White River beds, there can be very little doubt that *Miohippus* has descended from one or more species of *Mesohippus*; but if so, and unless the ancestral species of the White River genus has not yet been discovered, the principle must be admitted. The sulci which invade the articular surfaces of the tarsal bones, and are so conspicuous in the recent horses, have already commenced in *Mesohippus*. In that genus they are variable, but, so far as I have been able to observe, they are more constantly present and larger than in *Miohippus*, its successor. None of the known species of the latter genus fulfills all the conditions which are required of a form ancestral to *Anchitherium*. Some do so in one respect, others in another, none in all. If this alternation in minute details is to be rigidly excluded, I know of no species among fossil mammals which can claim to be ancestral to another, and unless, therefore, we are prepared to admit that no two species which have been found in successive formations stand in a direct relation of descent to one another, there would seem to be no escape from the conclusion that, in some cases at least, the general differentiation of a line may be

accompanied by an ebb and flow in certain minor characters, illustrating what Galton has called the "regression to mediocrity." This does not imply an all-round, indeterminate variation; the changes are alternately towards and away from a certain definite standard, and are sometimes repeated in one succeeding form after another, while in other cases a new set of characters are affected. Indeed, if we admit the possibility of parallel developments, and that, at least, is demonstrated by the fossils beyond peradventure, the possibility of alternations follows of itself.

While there is very little in favor of the view of indeterminate variation to be derived from a series of fossil mammals, yet *Anchitherium* does display some variations which appear to be of this character. Thus Filhol has noticed the instability of the tubercle which sometimes appears in the entrance to the median valley of the upper teeth. "Il semble qu'il n'y ait aucune tendance à des modifications de la structure des dents. Le seul fait que j'ai pu constater, et qui a une bien petite importance, consiste dans la présence ou l'absence d'un denticule d'émail qu'on trouve aux dents supérieures, entre les denticules internes. Sur la pièce que j'ai fait représenter on observe ce denticule sur les trois dernières prémolaires et sur la dernière molaire; sur un autre échantillon il existe sur toutes les dents, alors que sur deux autres il fait absolument défaut sur les molaires vraies" (No. 13, pp. 193, 194). In the specimen of *A. equinum* which I have described, a similar tubercle occurs in the posterior valley of the first lower molar, which is doubtless of the same variable character. In none of the equine genera do these tubercles attain any importance, and they have, therefore, the appearance of being indeterminate variations.

Another principle may be deduced from the facts of equine descent, viz., that a slight degree of specialization in a direction away from that taken by the main line is not incompatible with a place in that line. Thus the elbow joint of *Mesohippus* is curiously specialized in a fashion that does not occur in any of the later horses; the outer portion of the humeral trochlea projects laterally and is flared in a peculiar manner, forming with the corresponding surface on the radius a joint which allows an extraordinary degree of flexion. But for the obliquity of the trochlea, which throws the radius outward when the arm is flexed, the two bones could be brought into contact for almost their whole length without dislocation. It may be objected that no known species of *Mesohippus* is really in the direct series, and that the ancestral species did not have this peculiarity, but this seems improbable from many points of view, especially when it is remembered that a trace of the same structure may be observed in *Miohippus*. If true at all, this principle is of wide application, but it must not be pushed too far, for nothing seems better established than the belief that premature specialization in any conspicuous degree is fatal to the perma-

nence of a line, examples of which may be found abundantly in every horizon. In the case of *Anchitherium*, it may seem that I have excluded it from the main phylum on very trivial grounds, deviations which are no greater than the elbow joint of *Mesohippus*. But in the teeth of *Anchitherium* we find that characters which are constant in all the genera before and after it, characters in the continual development of which lies the peculiarity of the evolving equine dentition, are reduced or entirely lost. Of itself, perhaps, this fact would be insufficient to justify us in excluding the genus from the direct line, but it coincides, as we have seen, with many other facts, all of which point to the same conclusion.

The following table expresses concisely the relationships of the various Oligocene and Miocene equine genera, according to present information.

Loup Fork,	<i>Protohippus.</i>	<i>Hipparion.</i>
Deep River,	<i>Anchitherium.</i>	<i>Protohippus.</i>
(Hiatus),	? <i>Anchitherium.</i>	<i>Desmatippus.</i>
John Day,		<i>Miohippus.</i>
White River,		<i>Mesohippus.</i>

Rhinocerotidæ.

CÆNOPUS? Cope.

The rhinoceroses of the lower beds of the Deep River valley are represented in the collection only by some portions of mandibles which contain much mutilated teeth. These remains are altogether too uncharacteristic to admit of generic reference.

APHELOPS Cope.

Bull. U. S. Geol. and Geogr. Surv., No. 1, 1874, p. 13.

The upper beds yielded some fragmentary remains of a large rhinoceros which almost certainly belong to *Aphelops*. The best preserved of these is a portion of a skull, including the occiput, zygomatic arch and roof of the cranium, together with fragments of the molar teeth and superior maxillary bone, but, in the absence of

characteristic parts of the skull, the specific reference of this specimen is uncertain. The antero-posterior concavity of the upper profile of the cranium, and the rise towards the occipital crest, constitute a resemblance to *A. megalodus*, though these features are less emphasized than in that species. On the other hand, the projecting occipital condyles and long, laterally compressed postglenoid process, with its rugose posterior border, are rather more like those of *A. fossiger*. The posttympanic process of the squamosal does not quite reach the postglenoid, while in most specimens from the upper Loup Fork beds there is a more or less extensive contact between the two processes, though they do not seem to be coössified.

As I pointed out several years ago (No. 35, p. 16), the line of the horned rhinoceroses of the Old World diverged at an early period from the American hornless series; the two phyla cannot well have any common ancestor more recent than the Aceratheria of the White River Oligocene. It follows from this that those features in which *Aphelops* and its congeners resemble the modern genera more closely than do the White River species, have been independently acquired in the two lines. These resemblances are numerous and, because of the confidence with which we may regard them as parallelisms, worthy of enumeration.

The following brief summary of the points in which *Aphelops* approximates the modern standard more than do the White River forms is taken principally from the papers of Cope and Osborn upon that genus. (1) The increased size and robustness of the skeleton, as compared with that of the older genus, are very marked, and in some species (*e. g.*, *A. fossiger*) carried even beyond the condition of the recent species, so as to produce, as Cope has shown, the proportions of the hippopotamus rather than those of any recent rhinoceros. (2) The upper incisors are reduced to a single one in each premaxillary. In the Loup Fork genus, *Peraceras*, these teeth have been lost entirely, as in the recent African form, *Aelodus*. (3) The superior premolars have become more thoroughly molariform by the more complete separation of their internal cusps (deutero- and tetartocones). (4) The upper molars have increased in size and have become more complicated through the development of spurs upon the transverse crests. (5) The shape of the occiput is much more modernized than in *Cænopus*, and in most of the species the upper contour of the skull is concave, rising more or less steeply towards the inion. (6) The postglenoid and posttympanic processes of the squamosal are in contact. (7) The postglenoid is less like that of the tapir in character and has an elongated styliform shape, as in the recent rhinoceroses. (8) The sagittal crest is shorter and less prominent and the cranial cavity more rounded and capacious. (9) The foramen lacerum anterius and foramen rotundum have become confluent. (10) The foramen lacerum medium and foramen ovale are

much more closely approximated and sometimes confluent. (11) In the humerus, the deltoid crest is much better developed. (12) In the carpus, the magnum does not support the lunar anteriorly, and the latter element has shifted more completely upon the unciform. (13) The fifth digit is reduced to a nodular rudiment of the metacarpal. (14) "The femur of the species from the earlier formations may be readily distinguished from that of those of the later Tertiaries by the forms of both the extremities. In the *Aceratheria*, this bone resembles that of the tapirs in the form of the great trochanter. This process is produced at its external border, has a recurved apex, and encloses a deep trochanteric fossa. In *Aphelops* it is precisely as in *Rhinoceros*, obliquely truncate externally, without prominent apex or well-marked fossa. In the *Aceratheria* the inner crest of the rotular groove is but moderately prominent; in *Aphelops* and *Rhinoceros* it is greatly developed" (Cope, No. 4, p. 771^e). (15) The astragalus has become lower and broader and has a much more extensive bearing upon the cuboid, and the calcaneum is shorter and more massive.

With these resemblances, *Aphelops* presents many divergences from the true rhinoceros series, which Osborn has thus summed up: "The subtriangular shape of the scapula, the very elevated position and sessile character of the deltoid ridge of the humerus, the spreading manus, and the comparatively feeble development of the third trochanter of the femur" (No. 28, p. 98). To these may be added certain constant differences in the character of the skull. The presence of horns in one series and the absence of them in the other is doubtless the cause of these divergences in skull structure. Leaving out of view the problematical *Diceratherium*—a genus which is common to both hemispheres, and the relationship of which to the other genera of the family is still far from clear—all the American forms have weak and slender nasals; the sagittal crest is retained, in striking contrast to the broad, flattened cranium of the horned genera, and the development of air sinuses in the bones which surround the cerebral cavity is carried only to a moderate extent. Still farther differences between the two series occur in the details of the tarsus and the mode of articulation of these bones with the metatarsus.

It may be fairly concluded that the American hornless genera, while running parallel to the horned rhinoceroses of the Old World in many very striking ways, nevertheless form a series entirely independent of them.

ARTIODACTYLA.**Oreodontidæ.****MESOREODON** Scott.

Amer. Naturalist, 1893, p. 661.

Oreodonts with skull structure very similar to that of the John Day genus, *Eporeodon*, but with molars showing an incipient tendency to hypsodontism. Feet constructed as in *Merychyus*. Manus "adaptively" reduced, the third metacarpal articulating with the trapezoid. A rudimentary clavicle present. Larynx with ossified thyroid cartilage.

It may seem that this form is not generically separable from *Eporeodon*, and the relationship between the two is certainly very close; but if so, it must be given at least subgeneric rank. Animals of this type are much the most abundant fossils of the lower Deep River beds, outnumbering in wealth of individuals all the other species in the collection taken together. Two species are found in association.

MESOREODON CHELONYX Scott.

(*loc. cit.*)

Size exceeding that of *Eporeodon*, teeth large, zygomatic arches depressed, occiput drawn out into supero-lateral wings, metapodials rather short and stout, ungual phalanges trowel-shaped and pointed.

This species is very much the more abundant of the two and is represented in the collection by a large number of specimens, so that, with the exception of some vertebræ and ribs and the sternum, all parts of the skeleton may be described. A considerable degree of variation obtains among these specimens, both in regard to size and in other more important respects. Some of these differences, however, are almost certainly of a sexual nature, and they give no satisfactory reason for establishing another species.

I. *Dentition*. A. *Upper Jaw* (Pl. V, Fig. 36). The incisors have small and simple crowns, which are antero-posteriorly compressed and in the unworn state are somewhat pointed. In size, they increase regularly from the first to the third. The canine is of the ordinary trihedral recurved shape characteristic of the family, but differs from that of the older genera in having upon its inner face a deep groove, bounded before and behind by sharp enamel ridges.

The premolars are relatively larger than in *Oreodon* or *Eporeodon* and have a different external form, which constitutes an approximation to *Merychyus*. The change consists in an elongation of the crown, both vertically and antero-posteriorly,

in the disappearance of the median ridge on the outer side of the protocone, as well as of the external cingulum, of which a trace is retained on p. 4. The construction of the internal side of the crown is very much like what is to be found in *Oreodon*, but the ridges and hollows are, for the most part, better developed, and there are other minor differences. In all the premolars the protocone is a compressed and trenchant pyramidal cone, terminating below in an acute point which is in the median line of the crown. The first premolar has a slightly convex external face and is not so wide transversely as in the White River genus, especially in the posterior half; on the front edge there is a fossa bounded by an internal ridge which descends parallel to the edge of the protocone, and a faintly marked posterior fossa is formed by a slight elevation of the cingulum. This tooth is therefore of a somewhat different shape and simpler pattern than p. 1 of *Oreodon*. The second premolar is larger than p. 1, but has a similar external form with convex face; internally there are two anterior fossettes, the second of which is formed by the anterior cingulum, and the posterior fossette is much deeper than in p. 1. All of these internal ridges are more prominent than in the White River genus, but the transverse diameter of the crown is less. The third premolar has a slightly concave external face, and the internal crests and cingulum are better developed than in p. 2. The anterior ridges are more conspicuous than in *Oreodon*, but the posterior cingulum, or deuterocone, very much less so, and this, combined with the narrower crown, gives the tooth quite a different appearance in the two genera. In p. 4 we find the usual pair of crescents, the proto- and deuterocones, as in the selenodonts generally; the transverse width of the crown is somewhat greater in proportion, the protocone more compressed laterally and the valley narrower, though deep, than in *Oreodon*.

The molars are like those of *Eporeodon*, but with a certain resemblance to those of *Merychys*; this likeness is to be seen in a heightening of the crown vertically, narrowing of the valleys, the compression or thinning of the external buttresses (para- and mesostyles) and in the fore-and-aft extension of the postero-external crescent in m. 3. On the other hand, the characteristic feature of the *Merychys* molar, viz., the extension of the posterior horn of the crescentic protocone, cutting off the anterior horn of the hypocone from contact with the outer wall, is not present. In m. 1 and m. 2 the postero-internal crescent is developed at the expense of the antero-internal, which is especially small in m. 1, but in m. 3 the two are of nearly equal size and the adjacent horns are in close contact at their extremities. M. 3 has a well-developed outer fold or buttress at the hinder edge of the metaconid, which extends beyond the posterior horn of the inner crescent as in *Eporeodon* and *Merychys*, but not in *Oreodon*.

B. *Lower Jaw.* The incisors are smaller than in *Eporeodon* and have chisel-shaped crowns, with an internal cingulum upon the second and third; all three are of nearly equal size and are quite strongly procumbent. The canine is larger than the incisors, to which series it functionally belongs, and is, like them, quite procumbent.

The first premolar has the caniniform shape and function characteristic of all the genera of the family except *Pithecistes*; there is a very marked difference in the size and shape of this tooth in the various specimens, a difference which is doubtless sexual. In those skulls which are supposed to be of females, $\overline{p.1}$ is much lower and smaller, and in shape less completely caniniform than in the males. The other premolars in all the available specimens are so abraded that the details of their construction cannot well be made out; they are longer in the antero-posterior direction than those of *Eporeodon*, and $\overline{p.2}$ is implanted by two well-separated fangs. In $\overline{p.4}$, which is less rapidly worn down than the other premolars, there are two deep internal valleys, one in front of and the other behind the deuteroconid; the posterior valley becomes, on abrasion, an isolated fossette.

The molars are much more like those of *Eporeodon* than those of *Merychys* in the general shape of their broad, low crowns; but the valleys are narrow and soon disappear on wear, and the inner lobes are somewhat more flattened than in the John Day genus.

Measurements.

	MALE.	FEMALE.
	M.	M.
Upper molar-premolar series, length103	.101
Upper premolar series, length048	.048
Upper canine, antero-posterior diameter (fang)009	.008
Upper canine, transverse diameter (fang)012	.010
Upper first premolar, length010	.011
Upper second premolar, length013	.014
Upper third premolar, length013	.013
Upper fourth premolar, length012	.012
Upper fourth premolar, width014
Upper molar series, length055	.053
Upper first molar, length015	.012
Upper first molar, width015
Upper second molar, length018	.016
Upper second molar, width021
Upper third molar, length025	.024
Upper third molar, width025
Lower molar-premolar series, length107	.109
Lower premolar series, length048	.046
Lower first premolar, length010	.008
Lower first premolar, width009	.006

	MALE.	FEMALE.
	M.	M.
Lower second premolar, length.....	.013	.013
Lower third premolar, length.....	.013	.014
Lower fourth premolar, length.....	.015	.014
Lower molar series, length.....	.059	.064
Lower first molar, length.....	.014	.014
Lower second molar, length.....	.017	.018
Lower third molar, length.....	.028	.032

The *Milk Dentition* is like that of the older genera in that $\bar{d}.3$, which in *Merychys* is molariform and composed of four crescents, is like neither molar nor premolar. The anterior half of the crown is a compressed protocone with trenchant edges, like the corresponding cusp in the premolars, but thicker transversely, and with a fossette upon its anterior face. Except for its greater thickness, this portion of the crown is like the whole of $\bar{d}.2$ or the corresponding premolar. The posterior part of the crown is composed of a pair of transversely placed crescents, the trito- and tetartocones, and resembles half of a molar. As I have elsewhere pointed out, with reference to the more ancient members of the family, this tooth plainly shows that in the upper milk molars the homologies of the cusps, as determined by their position, are the same as in the premolars, but the order in which these cusps appear is altogether peculiar, being as follows: proto-, trito-, tetarto- and deuterocones (No. 29, p. 441). In the lower series, $\bar{d}.2$ and $\bar{d}.3$ are like their successors in the permanent dentition, while $\bar{d}.4$ is of the usual artiodactyl pattern, consisting of three pairs of crescents; of these, the anterior pair is formed by the paraconid and an element internal to it, to which, as it occurs only among the artiodactyls, I have not thought it worth while to give a special name. I cannot determine whether $p.1$ has a predecessor in the milk series, as it has in *Oreodon*, though there is some reason to think that this is the case. If so, the change takes place at an early period, before any of the other milk molars are shed. The milk canines and incisors differ from the permanent ones merely in size.

In short, the temporary dentition of *Mesoreodon* departs from that of *Merychys* more widely than does the permanent one, though in this connection it should be remembered that the temporary teeth are not known in the earlier species of this genus, *M. zygomaticus* and *M. pariogonus*, and as these species have a permanent dentition which in one or the other respect recalls that of the older genera, it may well happen that the temporary dentition of these species will also prove to be intermediate between that of the typical *Merychys* species from the upper Loup Fork and that of the more ancient forms of the family.

The Skull (Pl. IV, Fig. 32; Pl. V, Fig. 35). The structure of the skull is so

like that in *Eporeodon* that no detailed description of it will be necessary, and it will therefore suffice to mention the points of difference between the two genera. The general proportions of the skull, length of face and cranium, size and position of the orbits, etc., are very similar in both; it is only when we come to compare the details that differences become apparent. In *Mesoreodon* the anterior aspect of the premaxillaries is slightly broader and more flattened, and the two bones are more closely applied together and the symphyseal portion is more thickened. These changes are very slight, but they are not unimportant, since they are in the direction of the curious ankylosed premaxillaries of *Merychyus*. The maxillary sinuses are enlarged, which gives to the face a slightly swollen appearance. As in the older genera of the family, there appears to be a sexual difference in the lachrymal depression, the depth of which varies with the size of the canines, indicating that it was better marked in the males, but it is never so deep as in the males of *Eporeodon*. The frontal sinuses are more inflated than in the John Day genus, which gives to the forehead somewhat the same vaulted appearance as in *Merychyus*, but to a less degree; the nasal processes of the frontals are unusually long.

The zygomatic process of the squamosal is intermediate in character between that of *Eporeodon* and that of *Merychyus zygomaticus*; it is very widely expanded at the base, both transversely and antero-posteriorly, and its outer border is quite strongly raised, thickened and rugose, more so than in the former, less so than in the latter. The postglenoid process resembles that in the John Day form in being low, broad and very massive. The tympanic bullæ vary in size, being in some specimens much more prominent and inflated than in others. So far as the material in hand goes, it appears to indicate that the bullæ were more largely inflated in the male than in the female, but a much larger series of skulls will be required to definitely determine whether this is really a sexual character or not. The occiput is peculiar, and in its upper portion very similar to that of *Eporeodon*, the angles being extended into a pair of large wing-like processes as in that genus and in some species of *Oreodon* as well. These prominent processes are separated by a deep concavity; beneath this the surface is transversely very convex, prominent in the median line, and with deep grooves or narrow fossæ at the sutures between the squamosals and the exoccipitals. The wide transverse expansion of the latter elements makes the base of the occiput very broad. The paroccipitals are likewise broad at the base and closely applied to the bullæ, but the distal portion is slender and tapering. In these respects the inferior portion of the occiput is intermediate in structure and appearance between that of *Eporeodon* and that of *Merychyus zygomaticus*. As in the latter, the condyles project more posteriorly than in the John Day form.

The mandible is most like that of *Eporeodon*, but with some changes in the direction of *Merychys*. Owing to the procumbency of the incisors and their alveoli, the outline of the chin, when viewed from the side, is seen to be strongly concave. In *Eporeodon* the posterior margin of the angle and ascending ramus is regularly rounded and projects far back of the condyle, while in *Merychys zygomaticus* this margin is nearly straight and vertically directed and extends but little back of the condyle, from which it is separated by a notch. In *Mesoreodon* the shape of this region of the mandible is intermediate between these two extremes. The coronoid is short and slender, the sigmoid notch deep and widely open, and the condyle is much extended transversely.

By a happy accident the hyoid (Pl. III, Fig. 29) is preserved almost intact in one of the specimens and in its natural position. This apparatus in some respects differs from that of any known artiodactyl and agrees better with the hyoid of certain perissodactyls. No doubt can exist as to the proper reference of the specimen, as is demonstrated by its connection with the skull, which was that of a large male, as indicated by the robust canines.

The tympano-hyal is a short, stout, cylindrical bar, which is inserted into a depression upon the outer side of the auditory bulla. The stylohyal forms a long and broad (antero-posteriorly) but thin and very much compressed bar, which expands at the proximal end, but this portion is fractured, so that its exact shape cannot be determined. Except for this proximal expansion, the bone is of almost uniform size throughout. The epihyal is well ossified and relatively longer than in the sheep; it is narrower and somewhat thicker than the stylohyal and tapers distally. The ceratohyal is also better developed than in the modern ruminants; it is of a curious, paddle-like shape, slender and rounded where it joins the epihyal and expanding into a rounded blade posteriorly, where it is applied to the basihyal; it is not ankylosed with the latter. The basihyal is unlike that of any artiodactyl, with which I have been able to compare it, and much more resembles that of the horse. In shape it is narrow, depressed and thin and curved backward; *i. e.*, with the concavity towards the front. Its great peculiarity, for an artiodactyl, consists in the presence of a glossohyal process, which is given off from the middle line of the hinder border. This process is much shorter proportionately and more curved backward than in the horse, and is compressed antero-posteriorly instead of laterally. I can find no other artiodactyl in which this process occurs. The thyrohyals are ankylosed with the basihyal, at which points they form slight, club-shaped swellings; they are slender, rounded, arched somewhat anteriorly and are of unusual relative length, being nearly as long as the stylohyals, though of altogether different shape.

Posterior to the hyoid apparatus, but not directly connected with it, the matrix contains a hollow, compressed semicylinder, or spout-shaped piece of bone (Fig. 29, *T. c.*), with exceedingly thin walls, which, strange to say, is unmistakably the ossified thyroid cartilage of the larynx. The position and, still more, the shape of this bone do not admit of the least doubt as to its nature, and this is one more added to the many peculiarities of this very peculiar family, though whether the character is confined to the present genus or is common to many other members of the group is not known as yet. Obviously, only by the rarest chance could such a fragile structure be preserved. Possibly the ossification of this cartilage is a sexual character, for, as already mentioned, the skull with which the specimen was found associated is very probably that of a male. The function of this bone was probably similar to that performed by the enormously inflated basihyal of the howling monkeys, and must have given to these animals most unusual powers of voice. So far as I can discover, such ossification is not known elsewhere among the Mammalia.

There is no available material to compare the hyoid apparatus here described with that of the other genera of the family, since these bones are but rarely found in a fossil state. One specimen of *Eporeodon* from Oregon shows, however, that the stylohyal in this genus resembles in size and shape that of *Mesoreodon*.

Measurements.

	MALE.	FEMALE.
	M.	M.
Length of skull from summit of occiput to end of nose.....	.252	.248
Length from occipital condyles to incisive alveoli.....	.232	.234
Distance from summit of inion to base of lower jaw (vertical).....	.180	.187
Length of cranium from summit of inion to postorbital margin135	.133
Length of face from postorbital margin to end of nose.....	.126	.126
Height of occiput.....	.085	.078
Breadth of the same at base070	.070
Breadth of skull at zygomatic arches.....	.142	.142
Breadth of skull at postorbital arches110	.12
Breadth of face at upper first premolars.....	.049	.047
Breadth of face at last molars.....	.080	.085
Length of parietal crest.....	.098	.089
Length of frontals in median line.....	.050	.058
Length of nasals in median line.....	.100	.100
Breadth of face between frontal angular processes.....	.029	.033
Vertical diameter of orbit030	.039
Transverse diameter.....	.030	.030
Height of lower jaw at coronoid process096
Height of lower jaw at condyle.....	.090	.095
Height of lower jaw back of last molar.....	.049	.053
Height of lower jaw at third premolar.....	.031	.034

	MALE.	FEMALE.
	M.	M.
Breadth of lower jaw obliquely back of last molar073	.075
Length of symphysis of lower jaw.....		.052
Height of anterior nares.....	.035	.032
Breadth of anterior nares026	.032
Distance between the supraorbital foramina016	.024
Distance between the infraorbital foramina056	.060
Length of hard palate126
Width of hard palate between first molars.....		.045
Stylohyal, length.....	.050
Epihyal, length.....	.015
Ceratohyal, length019
Basihyal, width.....	.018
Thyrohyal, length.....	.040
Thyroid cartilage, height.....	.016

The Brain. Having no brain-cast of the John Day genus *Eporeodon* prepared, I am unable to compare that of *Mesoreodon* with it, and must therefore take the White River *Oreodon* as a standard. In the latter genus there is a considerable degree of individual variation, both in the shape of the hemispheres and in the number and extent of their convolutions. To some of these types the brain of *Mesoreodon* presents a much closer resemblance than to others, but is somewhat more advanced and modernized than any of them. This advance is noticeable in the general form of the hemispheres, which, though not broader behind than in some specimens of *Oreodon*, are much more so anteriorly, and thus the whole brain is fuller, more rounded and tapers less forward. The hemispheres have also slightly increased in vertical diameter, so that they are no longer exceeded in this dimension by the height of the cerebellum and medulla oblongata. Posteriorly, the two halves of the cerebrum are brought closer together and reach the cerebellum in the middle line, not gaping so as to expose part of the optic lobes, as is the case in the White River genus. They do not, however, appear to overlap the lateral lobes any more extensively than in that form.

The sulci are very nearly the same as occur in some specimens of *Oreodon*, but they pursue a slightly more sinuous course, which gives an appearance of richer convolutions. The dorsal surface displays (1) a short and straight lateral fissure, which does not connect anteriorly with the suprasylvian, as is sometimes the case in the White River genus. As regards the latter, Krueg (No. 22) regards this sulcus as the splenial, which by an extreme degree of "supination" is exposed upon the dorsal surface of the cerebrum, as in many of the small artiodactyls now living. But as this fissure does not extend to the medial surface of the hemisphere, this interpreta-

tion does not seem probable. (2) There is a longer and more curved suprasylvian fissure, which is connected anteriorly with the coronal fissure by means of a short and faintly marked ansate sulcus. This connection is also found in some specimens of *Oreodon*. (3) The coronal sulcus consists of two portions; the anterior is longer and curves downward and outward, while the posterior is shorter and more obscurely marked and converges towards the middle line in a way that suggests the crucial sulcus of the Carnivora. The lateral view shows, in addition to these fissures, a short and nearly horizontal sylvian sulcus and a presylvian which has a more nearly vertical course than in *Oreodon*. The sylvian fissure appears to be connected with the fissura rhinalis, though in this region the sulci are very obscure and difficult to interpret. Indications of a posterior suprasylvian sulcus are also to be observed.

The character of the cerebral sulci is, it is obvious, very much the same as that which occurs among the smaller and more primitive forms of existing ruminants, and these, as Krueg has shown, agree closely in fundamental plan with the Carnivora. As there is every reason to believe that the *Oreodontidae* are connected with the Pecora only through very ancient forms, in which the hemispheres were either smooth or but very little convoluted, this resemblance must be chiefly ascribed to parallelism of development. Still more obviously is this the case with regard to the likeness between these artiodactyls and the Carnivora.

In both of the brain-casts of *Mesoreodon* the olfactory lobes are broken away, but it is plain that they were not at all overlapped by the cerebrum. The cerebellum is very much as in the older White River type; its posterior face rises nearly vertically from the medulla; the vermis is large and prominent and the lateral lobes are broad. In neither of the specimens is the cerebellum sufficiently well preserved to display the details of the convolutions.

The Vertebral Column. The atlas is rather more like that of the true ruminants than is that of *Eporeodon*. This is due principally to the more uniform width of the transverse processes and their continuation into short spines behind the surfaces for the axis, from which they are separated by decided notches. This prolongation of the transverse processes is, however, much less marked than in the Pecora. On the other hand, the processes are more widely expanded laterally than in *Eporeodon*, which is a departure from the ruminant type. The anterior extension of the transverse process has, as in the earlier genera of the family, converted the atlanteo-diapophyseal notch into a foramen, but there is no perforation for the vertebrarterial canal. The anterior cotyli for the occipital condyles are deep and are more distinctly separated at their inferior borders than in *Eporeodon* and the neural spine is larger and

more rugose. The posterior articular surfaces for the axis are larger in both dimensions than in the latter genus, but especially in width.

The axis is very different from that of the Oregon genus. The atlanteal facets are broader and higher, descending more below the level of the centrum and separated by a more decided medio-inferior notch, but not, as is the case in *Eporeodon*, divided above by deep notches from the bases of the pedicels of the neural arch. The odontoid process is wider, more depressed and spout-like, with more elevated margins and with the articular surface for the inferior arch of the atlas rising higher upon its sides. The odontoid process is thus in an analogous stage towards the assumption of the spout-like character as it is in *Protolabis* among the camels and *Miohippus* among the horses. The transverse processes are longer and heavier than in *Eporeodon*. The neural spine is of very different shape from that of the latter, a change which is chiefly brought about by an elevation of the anterior portion, so that it forms a large hatchet-like plate, quite different from the spine found in the other members of the subfamily and more like that of *Agriochærus*. The postzygapophyses are more horizontal in position than in the Oregon genus, presenting more directly downward and less obliquely outward and backward. The pedicels of the neural arch are not perforated for the second pair of spinal nerves.

The remaining cervicals are rather short, with slightly opisthocœlous centra, which are keeled on the inferior side. The transverse process and pleurapophyseal plate are well developed and the latter reaches great size on the sixth vertebra. The neural spine is a mere ridge on the third, fourth and fifth cervicals, on the sixth it is much higher, slender and inclined forward, while on the seventh it is still higher and heavier. In proportion to the size of the head, the neck is of about the same length as in *Eporeodon*, but the vertebræ are more heavily built.

The thoracic vertebræ are not different in any very important respect from those of the Oregon genus, except for the better development of the spines. On the first of the series the spine is considerably higher and thicker than on the last cervical, but is much surpassed in both respects by the spine of the second, in which this process reaches almost bovine proportions. The other anterior thoracic vertebræ have broad, compressed spines, though none of the specimens are sufficiently complete to allow a determination of the length of these processes.

The remaining regions of the vertebral column are represented by numbers of isolated centra, from which the processes have been broken away, and which therefore do not require any detailed description. So far as they go, these bones differ but little from the corresponding vertebræ of *Eporeodon*.

The anterior ribs are rather short, broad and compressed, and of triangular

section; posteriorly, they become longer, much more slender and of more rounded section. Nothing is known of the sternum.

The *Fore Limb* displays some characters of unexpected interest. The scapula varies considerably in the different specimens, some of which variations would appear to be of a sexual nature.

The best preserved shoulder-blade (Pl. IV, Fig. 33) is one which belonged, as I believe, to a female, being associated with a skull in which the small size of the canines and the caniniform first lower premolar is very striking. In this specimen the coracoid and suprascapular borders are broken in such a way as to prevent an accurate determination of the outline of the bone, but the spine, neck, and most of the postscapular fossa are in good condition. The glenoid cavity is small, shallow, and of nearly circular shape, the antero-posterior diameter but slightly exceeding the transverse. The coracoid is large, especially in the vertical dimension, but is not clearly demarcated from the neck of the scapula and displays but little rugosity; hence it is not conspicuous when viewed from the outer side. The neck of the scapula is high in the vertical direction, narrow and contracted, and the rugose lines for muscular attachment are but faintly marked. Above the neck, the glenoid border extends obliquely upward and backward, enclosing with the spine a narrow, triangular postscapular fossa. This border is considerably thickened and its external margin is elevated, making the fossa quite concave antero-posteriorly. The spine is very high, and for most of its length curved backward, so as to make the anterior surface convex and the posterior concave. Its free margin is flattened and gradually becomes wider inferiorly to the point where it sends out a distinct metacromial process. No other genus of the family has yet been found in which a metacromion occurs. Beneath this process the curvature of the spine is reversed, the posterior surface now being convex and the anterior concave, and the acromion projects forward as well as downward. The length of the acromion cannot be definitely stated, as its tip is broken away, but obviously it could not have descended nearly to the level of the glenoid cavity.

This spine is of a very exceptional character for an artiodactyl. In *Oreodon* there is no metacromion, the spine is lower and not recurved and descends more nearly to the level of the glenoid cavity. In *Eporeodon* there is likewise no metacromion, but the spine is very high and curved in very much the same fashion as in *Mesoreodon*.

The second specimen (Pl. IV, Fig. 34) has lost the spine but preserved the entire outline of the scapula, which is represented either by bone or by the impression of it in the matrix. There is good reason to believe that this specimen should be referred

to the same individual as a large male skull which was found in the same locality, but on this point I cannot speak with entire confidence. The glenoid cavity is somewhat larger and more oval in shape than in the specimen first described, the antero-posterior diameter distinctly exceeding the transverse; the neck is broader, heavier and less contracted, and has well-marked rugose lines for the attachment of muscles. On the other hand, the glenoid border is less elevated and the postscapular fossa is, in consequence, less concave. The coracoid border curves forward much more decidedly than it does in the scapula of *Oreodon*, making the proximal portion of the blade relatively much wider than in that genus. The suprascapular border is gently arched, but nevertheless forms nearly a right angle with the glenoid border. The spine is almost median in position, giving pre- and postscapular fossæ of nearly equal size, but of different shape, owing to the different course taken by the coracoid and glenoid borders.

The block of matrix which contains the scapula just described, holds also the last four cervical and first four thoracic vertebræ, with their ribs attached, and the proximal half of the humerus. The same block contains also a small bone (Fig. 34, *cl*) which is removed but a short distance from the coracoid process of the scapula, and runs forward and inward, overlapping the first rib and the transverse process of the seventh cervical vertebra. *This bone I regard as a rudimentary clavicle.* Naturally, such identification will be received with much doubt, and I was at first very skeptical about it myself. It is certainly most unexpected to find this element in an ungulate so far advanced in differentiation and so high in the geological scale as the middle Miocene, while it has not yet been detected in the Condylarthra of the lower Eocene. Nevertheless, in spite of the *à priori* improbability of the occurrence of the clavicle in a Miocene artiodactyl, there seems to be but little doubt that such is actually the fact. In the first place, the position taken by the bone in question is such as a clavicle would occupy if it were present. There is a slight vertical displacement of the whole fore limb and shoulder girdle, but otherwise the bones of all the surrounding parts—vertebræ, ribs, scapula and humerus—are in their natural position almost as perfectly as in a living animal. (2) There is no other bone in this skeleton with which this one can be identified; it is much too slender to be a part even of the smallest rib, and its shape is quite different from that of any of the elements of the hyoid apparatus. Fortunately, we already possess the latter belonging to (presumably) the same individual and can definitely state that the bone in question cannot be referred to it. (3) The shape is that which we should expect to find in a rudimentary clavicle; it is slightly arched downward, is very slender and of rounded section, with an inferior keel, which is best marked in the middle and dies

away towards the ends. (4) The unusual development of the spine of the scapula is an indication that the clavicle had not been entirely lost. (5) Wineza's observation (No. 36) that a transitory rudiment of a bony clavicle is developed in the sheep, points to the conclusion that this element has not been eliminated from the artiodactyls for so long a period as has been generally supposed. (6) Admitting that the structure under discussion really represents the clavicle, its very small size and loose attachments (for it is in contact with neither the scapula nor the sternum) will explain why it has not yet been observed in the more ancient forms of ungulates. Only by the rarest chance could such a bone be preserved in its natural position.

Unless, therefore, we are prepared to assume that a single bone of some small animal has become accidentally entangled with this skeleton of *Mesoreodon*, and in such a way as to exactly simulate the position of the collar bone, which is certainly highly improbable, there would seem to be no escape from the conclusion that the clavicle was present in this genus. However, other specimens will be required before we can be entirely satisfied on this point.

In this connection it may be noted that the simpler and less developed scapular spine of *Oreodon* would lead us to infer the absence of a clavicle in that genus. But, assuming this to be the case, we cannot yet determine the significance of the fact since so little is known of the skeleton of those White River species in which the tympanic bullæ are inflated and which are presumably the ancestors of *Eporeodon*. In the absence of knowledge on this point we cannot tell whether the supposed clavicle of *Mesoreodon* should be regarded as a persistent rudiment or as a case of reversion and the reacquisition of a lost structure. The former alternative would certainly seem to be more probable, and, if it is true, it may serve to explain the very general difference between artiodactyls and perissodactyls with regard to the development of the acromion. As is well known, this structure is in nearly all artiodactyls large and prominent, while in even the Eocene perissodactyls the acromion is absent. If we may assume that the clavicle persisted longer in the former group than in the latter, this difference would be accounted for.

The humerus (Pl. IV, Fig. 34; Pl. V, Fig. 37) is in general very similar to that of *Eporeodon*, but has a decidedly stouter shaft; the head is more convex and presents much more posteriorly, less exclusively in the proximal direction. The external tuberosity is of a different shape, its extremities being less produced as overhanging hooks; the internal tuberosity is also less developed, and in consequence the bicipital groove is not so deep. The length of the shaft is about the same as in *Eporeodon*, but the diameter, both transversely and antero-posteriorly, is much greater. The distal end is of the shape which is characteristic and constant throughout the family.

This shape is already well shown in the White River species and is marked by its relatively great transverse breadth, prominent internal epicondyle, broad, rounded intercondylar ridge, which is nearly median in position, and the nearly equal width of the external and internal divisions of the trochlea. The anconeal fossa is relatively higher and narrower than in *Eporeodon*.

Some differences, which are probably of a sexual nature, are to be observed in the proximal end of the humerus in different specimens. In those which are associated with the skulls marked by small canines, and therefore presumably female, the head is more hemispherical and markedly shorter in the antero-posterior direction; the external tuberosity extends less completely across the anterior face of the bone and the bicipital groove is wider. Possibly, however, these distinctions are specific rather than sexual.

The ulna and radius (Pl. V, Fig. 38) are massively constructed; they are entirely unreduced and show no tendency to coössify at any point. The radio-ulnar arch is very long, extending from a short distance below the head to the distal expansion; this is not visible in the anterior view. The radius has the form of head which is characteristic of the family and therefore requires no detailed description. The shaft is not so broad and antero-posteriorly compressed as in *Eporeodon*, but more rounded and cylindrical in the middle, reverting thus in some degree to the condition found in *Oreodon*. The distal end is more expanded transversely than in *Eporeodon*, though in this respect there is considerable variation. The scaphoid surface is peculiar in the deep groove on its ulnar border. This is already indicated in the Oregon genus, but to a much less conspicuous degree, especially in the breadth and depth of the groove behind. A similar groove appears in *Merychys*. The lunar facet is like that of *Eporeodon*, but is less closely connected with the scaphoid facet.

The ulna is quite unreduced and has a very heavy shaft, which almost equals that of the radius in antero-posterior thickness and exceeds it in width. The olecranon is high and massive. The distal end is excavated to receive the expansion of the radius and carries a facet for the cuneiform, which is narrow antero-posteriorly but broad transversely. This ulna differs but slightly and in no important respect from that of *Eporeodon*.

The manus (Pl. V, Figs. 39, 40) presents some features of much interest, as here we find most strongly emphasized the tendency towards *Merychys* which is more obscurely indicated in the structure of the skull and teeth. In the carpus the scaphoid has undergone some noteworthy changes as compared with that of the more ancient genera. It is increased in size, especially in breadth; the radial surface is, as usual, concave behind and convex in front, but rises more towards the ulnar bor-

der to enter the groove on the radius already mentioned. The ulnar side of the scaphoid is concave and is chiefly occupied by the large inferior facet for the lunar. The distal side is taken up by two facets, those for the magnum and trapezoid respectively. The magnum facet is the larger of the two and is deeply excavated behind, but descends abruptly in front. The lunar is both high and broad; its radial surface is saddle-shaped, concave from side to side and convex fore and aft, broad in front, much contracted and tapering behind. The radial side carries two facets for the scaphoid, the upper one small and nearly plane, the lower very large and convex and separated from the magnum surface by a scarcely perceptible ridge. The latter facet is almost entirely lateral, except on the palmar border, where it is reflected underneath so as to be partly distal. The unciform facet is concave and obliquely placed; it forms with the magnum surface a sharp beak, which is wedged in between the magnum and the unciform and extends nearly to the third metacarpal.

The cuneiform is broad and low and has a less dorso-palmar diameter than the other proximal carpals. The ulnar surface is a narrow groove which is reflected down upon the external side of the bone, and the pisiform facet forms a broad band upon the palmar side which is continuous with the ulnar facet. Distally, the cuneiform displays a simply concave facet for the unciform. The pisiform is intermediate in character between the condition found in the earlier and that in the later genera of the family, being more expanded at the free end than in the former, less so than in the latter. The proximal end is much contracted and bears a single rounded articular surface, part of which is for the ulna and part for the cuneiform.

The trapezium is a small nodular bone which has but two facets, one for the trapezoid and, at an obtuse angle with this, another for the second metacarpal. This species and *Merycochoerus montanus* are the only members of the family in which I have succeeded in obtaining the trapezium, though the facets on the neighboring bones leave no room for doubt as to its presence in the other genera as well. This carpal enables us to state with entire confidence that in *Mesoreodon* the pollex is not represented even by a rudiment. The trapezoid is a large bone both vertically and transversely, but it has no great antero-posterior depth; proximally, it bears a large and simply convex facet for the scaphoid and its radial side is occupied by a concave surface for the trapezium. Distally, there are two facets, one of which is large and slightly concave, the other small, plane and inclined at an open angle to the first; the former is the surface for the second metacarpal and the latter for the third.

The magnum is a very characteristic bone, resembling strongly that of *Merychius* and *Merycochoerus*, though its peculiarities are not carried to such an extreme. Seen from the front, the magnum appears to be smaller than the trapezoid, and is

both lower and narrower, but its upper surface rises rapidly towards the palmar side, forming the "head." Behind the anterior face the bone is deeply constricted by two concave facets, one on the radial side for the trapezoid and the other on the ulnar side for the lunar. The trapezoid and magnum are very closely interlocked and form a continuous saddle-shaped surface for the scaphoid, which in appearance resembles the astragalar trochlea of a carnivore. The magnum, including even the head, is entirely beneath the scaphoid, the opposite condition to that of the horse, in which the head is entirely underneath the lunar, though the scaphoid rests upon the anterior portion. The lunar surface is deeply concave (though less so than in *Merychius* and *Merycochaerus*, in which it describes a semicircle) and almost entirely lateral in position, but on the palmar side is a small, shelf-like projection which extends somewhat beneath the lunar. This gradual displacement of the magnum towards the radial side of the carpus is already indicated in the oldest known genus of the family, *Protoreodon*, and is more decidedly marked in *Oreodon* and *Eporeodon*, though even in the latter it has by no means been carried to the same extent as in *Mesoreodon*, in which it attains almost the extreme position found in *Merychius* and *Merycochaerus*. The contact between the magnum and the unciform is very slight and nearly or quite limited to the posterior or palmar margin, the two bones being separated by the long beak of the lunar and the strong process which the third metacarpal sends obliquely upward and outward to abut against the unciform. Distally, the magnum bears a single saddle-shaped facet for mc. iii, which is reflected upward more upon the ulnar than on the radial side. This facet is elongate and quite deeply concave in the dorso-palmar direction, contracting to a point behind, narrow and very convex transversely. There is no facet for mc. ii, that bone being excluded from contact with the magnum by the connection of mc. iii with the trapezoid. The posterior hook of the magnum is short, curved, blunt, depressed and curved towards the radial side. The unciform is high and broad, with its proximal portion contracting posteriorly. The upper surface bears an oblique facet for the lunar, which rests almost entirely upon the unciform, and somewhat larger convex facet for the cuneiform. The metacarpal surfaces form a nearly continuous curve. On the radial side, though confined to the dorsal half of the bone, is a large oblique facet for the projection from mc. iii; distally, there is a larger facet for mc. iv and a smaller one for mc. v; the latter surface is reflected up upon the ulnar side of the unciform.

The metacarpals are four in number and in their proportions very similar to those of the older genera, *Oreodon* and *Eporeodon*, though differing in some important respects from the metacarpals of those genera in their mode of articulation with the carpus, which is like that of *Merycochaerus* and *Merychius* in being of the "adaptive"

type. In the second species of *Mesoreodon*, *M. intermedius*, to be described hereafter, the proportions of the metacarpals are more like those of *Merychys*.

The second metacarpal is short and slender, with a trihedral recurved shaft; the head is rather broad and bears a triangular, nearly plane facet for the trapezoid and a postero-internal one for the trapezium. This bone does not reach the magnum, which constitutes an important difference from the manus of *Eporeodon*, in which, as in the more ancient genera, mc. ii is in contact with the magnum. The third metacarpal is likewise different from that of the last-named genus; the head is expanded and deeply concave transversely and convex antero-posteriorly; on the radial side is a very small oblique facet for the trapezoid and on the ulnar side a very large one for the unciform. Both of these surfaces are confined to the anterior half of the metacarpal. Beneath the unciform projection on the head of mc. iii the bone is excavated to receive the head of mc. iv; posterior to this, and separated from it by a deep sulcus, is a second facet placed on a projection, which extends towards the ulnar side. This facet is somewhat oblique and extends *beneath* the head of mc. iv and the two bones are thus interlocked in a very complex and perfect manner. The same arrangement is indicated in *Oreodon*, but in this genus the posterior facet is much less conspicuously developed. In the present species, the shafts of mc. iii and mc. iv are quite heavy and not very long, in which respect they differ very markedly from those of the second species, *M. intermedius*. In *Oreodon*, mc. iii not only rises above mc. iv but also extends below it distally, while in *Mesoreodon*, as in *Merychys*, mc. iv extends slightly below the end of mc. iii, though it is considerably the shorter of the two. Proportionately, mc. iv is little, if any, longer in *Mesoreodon* than in the White River genus, the different disposition of the metacarpals being due to the enlarged unciform process of mc. iii, the greater relative height of the unciform, and the consequent downward displacement of the head of mc. iv.

The fifth metacarpal is quite different from that of *Oreodon* in having a narrower but deeper head, with the shaft broader proximally, expanding less distally and being more strongly recurved. In length and thickness it is the counterpart of mc. ii, whereas in the White River genus the latter is decidedly stouter. On all of the metacarpals the distal carinæ are much better developed than in *Oreodon* and are plainly visible when the manus is viewed from the front.

The phalanges of the proximal row are like those of the earlier genera of the family, except that they are relatively shorter. Those of the second row are notably shortened and broadened; the distal trochlea is wider and not reflected so far upon the dorsal side of the bone, but is more prominent upon the palmar side. The ungual phalanges of this species are very peculiar and different from those of any other

member of the family. They are wide proximally and taper distally to a point, which is more acute than in the other genera; in the median pair (digits iii and iv) the approximate borders are straight and the opposed borders curve distally towards the median line. Proximally, the ungual has considerable vertical depth, but this diminishes rapidly towards the distal point, and the dorsal surface is very convex and strongly arched from side to side. The unguals of the lateral digits are like those of the median pair, except for their very much smaller size. In brief, the ungual phalanx is shaped like the half of a slender and somewhat irregular cone.

Measurements.

	MALE.	FEMALE.
	M.	M.
Scapula, height.....	.138	.140
Scapula, greatest width.....	.088	.090
Scapula, width of neck.....	.023	.021
Glenoid cavity, antero-posterior diameter.....	.027	.022
Glenoid cavity, transverse diameter.....	.025	.022
Humerus, length.....		.151
Humerus, antero-posterior diameter of proximal end.....	.056	.049
Humerus, transverse diameter of proximal end.....	.042	.039
Humerus, width of distal end.....		.039
Clavicle, length.....	.027
Radius, length.....		.137
Radius, width of proximal end.....		.027
Radius, width of distal end.....		.029
Radius, width of shaft in middle.....		.014
Ulna, length.....		.180
Ulna, height of olecranon from sigmoid notch.....		.030
Ulna, breadth of shaft in middle.....		.016
Ulna, breadth of distal end.....		.014
Scaphoid, height.....	.016	
Scaphoid, width of proximal end.....	.012	
Lunar, height.....	.017	
Lunar, width of proximal end.....	.012	
Pisiform, length.....	.023	
Metacarpal ii, length.....	.054	
Metacarpal iii, length (not including unciform process).....	.065	
Metacarpal iii, width of proximal end.....	.016	
Metacarpal iii, width of distal end.....	.014	
Metacarpal iii, width of shaft below head.....	.013	
Metacarpal iv, length.....	.061	
Metacarpal iv, width of proximal end.....	.013	
Metacarpal iv, width of distal end.....	.012	
Metacarpal iv, width of shaft below head.....	.012	
Metacarpal v, length.....	.052	
First phalanx of third digit, length.....	.021	

Second phalanx of third digit, length.....	.013
Third phalanx of third digit, length017
Third phalanx of third digit, width of proximal end.....	.009

The Hind Limb presents fewer peculiarities than the fore limb, and, except in a few details, is very similar to that of *Eporeodon*. The pelvis (Pl. VI, Figs. 46, 47) is very like that of the Oregon form but with some minor differences. The ilium has a shorter peduncle which expands more abruptly into a wider plate. The latter is less strongly everted, especially at the antero-inferior angle, which is less prolonged. The iliac surface is broader and more rounded, the acetabular border less prominent, and the pubic border more so. The pit for the rectus femoris muscle is larger but not so deep. The acetabulum is much larger and relatively shallower and the articular surface is more reduced by the very large sulcus for the round ligament. The ischium is more twisted upon itself, so that the posterior end is much more everted and depressed. The crest above the acetabulum descends more abruptly in front and dies away behind without forming an ischiadic notch. The pubis in its free portion is short and stout and the symphysis, in which the ischium shares, is elongate.

The femur shows analogous differences from that of *Eporeodon*. The head is distinctly larger and more sessile and has an unusually anterior position; it does not rise so far above the bridge connecting it with the great trochanter. This bridge is more thickened in the antero-posterior dimension and the great trochanter is larger and more massive. The shaft is heavier and more arched forward and, distally, is both broader and deeper. The external linea aspera appears to be less conspicuously marked and the pit for the plantaris muscle shallower. The condyles have a greater vertical diameter but do not present so strongly backward. The rotular trochlea is wider; its margins are of equal height and more compressed.

The tibia is very much alike in the two genera. In *Mesoreodon* the external surface for the femoral condyle is broader and the cnemial crest more massive and rugose; the shaft is slightly heavier and the distal end rather more expanded, both transversely and from before backward. The grooves for the astragalus are wider and the intercondylar ridge broader and lower and not forming, as in *Merychys*, a posterior tongue. The sulcus which invades the external astragalar groove is larger and deeper, and the external groove is a little wider relatively to the internal than in *Eporeodon*. An important change which is already indicated in the Oregon genus is carried farther in *Mesoreodon*, viz., the presence of a *distal* facet for the fibula, showing that the latter has extended slightly beneath the tibia. I cannot ascertain the condition of the older species of *Merychys* in this respect, but in a specimen belonging probably to *M. elegans*, from the upper Loup Fork, there is no fibular facet

on the distal surface of the tibia and the surface on the external side is much larger and more deeply impressed.

The distal end of the fibula is preserved in one specimen; it forms a very large and heavy external malleolus which is especially expanded antero-posteriorly; on the distal side is a very long facet for the calcaneum, with the outer border somewhat elevated. On its inner surface the malleolus displays a projection which extends beneath the facet already described on the distal aspect of the tibia. The shaft was obviously reduced to the most slender proportions, though we cannot determine whether it was interrupted or entire.

The pes (Pl. V, Figs. 41, 42) requires but a brief description, as it departs very little from the type common to nearly all the members of the family, there being less variation in the structure of the hind foot than of the front. The calcaneum has a long and stout tuber, with nearly parallel borders, and thickens at the free end into a heavy knob; the fibular facet is low but very long, in which respect it differs strikingly from that of *Merycoidodon*. The distal astragalar facet is very long, but, as in nearly all the genera of this family, the sustentaculum projects but very little. The cuboidal surface is narrow but long, measured from the dorsal to the plantar edge.

The astragalus is low and broad; the outer proximal condyle exceeds the inner considerably in size, but less than in *Oreodon*, and is invaded by a larger sulcus; it has a more thickened and gently rounded external border than in that genus and the intercondylar groove is wider and less angulate. The navicular surface is very different from that of the White River genus, extending higher up upon the anterior face of the bone and having decidedly greater dorso-plantar thickness. Corresponding to the structure of the calcaneum, the sustentacular surface is long, narrow, and not connected with other facets. The cuboid, compared with that of the earlier genera, has increased in relative height, which gives it an appearance quite like that of *Merychius*, though it has not attained such an extreme; the calcaneal facet differs from that of *Merychius* and resembles that of *Oreodon* in being incised lower down upon the anterior face of the cuboid. The navicular has undergone no important changes, unless the greater elevation of its antero-external border be so regarded; the posterior hook is very long. The cuneiforms are very much as in the older genera. As in all the members of the family, the ecto- and mesocuneiforms are coössified, the compound bone differing from that of *Merychius* (at least of such species as *M. elegans* and *M. arenarum*) in its much greater proportional transverse width.

The metatarsals resemble those of *Oreodon*, but some changes may be observed which point in the direction of *Merychius*. Thus, the metatarsals are straighter, less

arched forward and more slender in proportion to their length; the distal carinæ are more prominent and more extended upon the anterior face of the trochlea.

The phalanges (Pl. V, Fig. 42) of the pes are like those of the manus, except for their greater size, and the curious, trowel-shaped unguals have their peculiarities somewhat emphasized.

Measurements.

	M.
Diameter of acetabulum, fore and aft.....	.029
Diameter of acetabulum, vertical.....	.028
Width of pelvic opening at pubes.....	.059
Femur, length.....	.190
Femur, width of proximal end.....	.050
Femur, diameter of head, fore and aft.....	.025
Tibia, length.....	.177
Tibia, breadth of proximal end.....	.044
Tibia, breadth of distal end.....	.028
Astragalus, length.....	.035
Astragalus, width of proximal trochlea.....	.020
Calcaneum, length.....	.064
Cuboid, height.....	.020
Metatarsal iv, length.....	.075
Metatarsal iv, width of proximal end.....	.013
First phalanx of third digit, length.....	.022
First phalanx of third digit, width of proximal end.....	.013
Second phalanx of third digit, length.....	.012
Third phalanx of third digit, length.....	.016
Third phalanx of third digit, width of proximal end.....	.013

MESOREODON INTERMEDIUS Scott.

Amer. Naturalist, 1893, p. 661.

This species is represented by foot-bones belonging to two different individuals, which are so different in their proportions from those of the foregoing species that they must be referred to another animal. The only skull which can with any probability be regarded as belonging to *M. intermedius* is a small one belonging to a very immature individual and therefore of little value for systematic purposes. The milk teeth are still in place, the permanent canines just beginning to appear, and the first permanent upper molar already protruded. This latter tooth is somewhat like that of *Merychys* in the shape of the external crescents and in the rapid narrowing of the valleys towards the base of the crown. The inner crescents, however, are not like those of the Loup Fork type.

One of the typical specimens (Pl. V, Fig. 43) consists of the third metacarpal entire and the proximal three-quarters of the fourth. As compared with those of

the preceding species, these bones are decidedly longer and more slender, with the carinæ of the distal trochleæ more extended anteriorly. In their proportions and in their carpal facets these bones closely approximate those of *Merychyus*, though the trapezoid facet of mc. iii is smaller.

The second specimen (Pl. V, Fig. 44) consists of isolated phalanges. Those of the proximal row are much more slender and arched forward than in *M. chelonys*. The unguals are extremely like those of *Merychyus*, but are somewhat more obtusely pointed.

Measurements.

	M.
Metacarpal iii, length069
Metacarpal iii, width of proximal end.....	.015
Metacarpal iii, width of distal end.....	.014
Metacarpal iii, width of shaft below head011
Metacarpal iv, width of proximal end013
Metacarpal iv, width of shaft below head.....	.011
First phalanx of third digit, length (pes).....	.023
First phalanx of third digit, width of proximal end012
Third phalanx of third digit, length.....	.017
Third phalanx of third digit, width of proximal end.....	.008

MERYCHYUS Leidy.

Proc. Acad. Nat. Sci. Phila., 1858, p. 24.

MERYCHYUS ZYGOMATICUS Cope.

(Syn. *Ticholeptus zygomatus* Cope, *Amer. Naturalist*, Vol. XII, p. 129.)

The type specimen of this species is a much crushed and distorted skull, of which, through the courtesy of Prof. Cope, I present a drawing (Pl. V, Fig. 45), corrected so far as is possible by the aid of other material. On comparing this skull with that of *Mesoreodon*, we are at once struck by the great increase in vertical height, both relative and actual, which it has undergone, the height measured vertically from the lower border of the mandible to the upper line of the forehead above the orbit being to the total length of the skull about as 7:11, while in *Mesoreodon* the height barely exceeds one-half of the length. The face has also become somewhat shortened and the cranium relatively longer. The orbits do not extend so nearly to the upper line of the skull, the forehead rising much more above them and is more convex, which appears to be due to a greater development of the frontal sinuses. The supraorbital ridges converge less rapidly, and the forehead is thus longer, higher and more arched, and the sagittal crest is shorter. The upper contour of the skull is more arched from before backward, and in all probability the great

posterior wing-like prolongations of the parietals and supraoccipital are much reduced. The occipital condyles project much more strongly backward and somewhat more downward. The paroccipital processes are much wider, at least at the base, where they form broad, thin, antero-posteriorly compressed plates. The notch between the postglenoid and posttympanic processes of the squamosal is greatly widened, especially above; below, it is narrowed by the downward and forward course taken by the posttympanic. This change is accompanied by another in the position of the external auditory meatus, which is "directed posteriorly in a way quite peculiar, resembling somewhat the position seen in some of the hogs" (Cope).

The zygomatic process of the squamosal has a more massive and rugose external border and its posterior expansion is directed more horizontally and less vertically than in *Mesoreodon*, and in the latter respect this species departs considerably from the other species of *Merychyus*. In spite of this difference, there is a very suggestive resemblance between the present species and *Mesoreodon* in the appearance of the zygoma. The malar is heavier and has greater depth beneath the orbit. The maxillary has a shorter but much higher facial portion and the ridge which runs forward from the malar suture is much better marked. In the type specimen, the region about the infraorbital foramen is much injured, but there is some reason to think that the foramen is double, and a facial vacuity is obviously present, and though its shape and size cannot be accurately determined, it was probably small and fissure-like.

The premaxillaries are coössified and have their anterior faces much flattened; the ascending rami are much shorter than in *Mesoreodon* and the anterior nares lower and more obliquely inclined upward and backward. The muzzle is relatively broader, but the increase in height of the alveolar portion of the premaxillaries and in breadth of their ascending rami, contracts the narial opening, especially in its inferior portion, where it becomes very narrow.

The mandible is different from that of *Mesoreodon* in several important respects. The horizontal ramus is proportionately shorter, but of greater and more uniform vertical depth, tapering less anteriorly; the chin is straighter and less concave when seen in profile and the incisive alveolus less depressed and procumbent. As in *Mesoreodon*, the anterior mental foramen is placed beneath $\overline{p. 3}$, whether, as in that genus, there is a second foramen underneath $\overline{m. 1}$, the specimen is too much fissured to show with clearness, though this appears to be the case. The angle projects somewhat below the inferior border of the horizontal ramus and its posterior margin is more thickened and rugose; on the other hand, it projects more behind the condyle, from which it is separated by a more decidedly marked notch. The masseteric fossa is notably smaller and does not descend so low upon the side of the jaw.

The extreme fragility of the type specimen and the hardness of the cement-like matrix in which it is imbedded have prevented the complete exposure of the teeth, so that these can be studied only from the external side, and important questions as to the constitution of their crowns must be left undecided. In the other specimens of the species at my command, the teeth are so badly preserved as to be of no value in this connection. The first and second upper incisors are very small, the lateral much exceeding the others in size, and the second somewhat larger than the median. These teeth, except for the greater relative size of the lateral one, closely resemble the incisors of the immature skull mentioned above and referred doubtfully to *Mesoreodon intermedius*. The canine is of the type usual in the family. The premolars have increased in vertical, but diminished in antero-posterior diameter; their front and hind margins are nearly parallel and the acute apex in each tooth is in advance of the median vertical line of the crown. Thus the postero-inferior cutting border is longer than the antero-inferior. In *Mesoreodon* the apex is in the middle line and the inferior trenchant margins are of subequal length. The molars exhibit the same reduction in length (antero-posteriorly) and increase in height as do the premolars, and are almost as distinctly hypsodont as are the molars of the later species of *Merychys* from the upper Loup Fork. The external pillars, especially the median one (mesostyle), are thin and compressed, but very prominent. The postero-external crescent is much more extended from before backward than the antero-external one, though the disproportion is less than in *Mesoreodon*.

The lower incisors are larger and, in particular, higher than the upper ones, and have compressed chisel-shaped crowns; the canine is broader than the incisors but has lost its typical shape. The caniniform first premolar calls for no remark, as it departs in no way from the shape common throughout the family. The second and third premolars resemble those of the upper jaw in their reduced length and increased height and in having their apices in front of the middle line of the crown. In $\overline{p.4}$ the heel (metaconid) is very distinctly separated from the protoconid, but is relatively smaller than in *Mesoreodon*. The lower molars are so concealed in the matrix that little can be made out with regard to them. As compared with the corresponding teeth of the older genus, they have shorter but much more decidedly hypsodont crowns.

MERYCHYUS PARIOGONUS? Cope.

Proceedings Amer. Philos. Soc., Vol. XXI, p. 542.

In the Princeton collection is the facial portion of a skull, which was found by Mr. Benet in the upper series of beds in the Deep River valley, and which clearly

belongs to *Merychys*. It may be provisionally referred to *M. pariogonus* Cope, though unfortunately a comparison with the type specimen is of little service, for the two skulls have almost nothing in common. In the type specimen, the cranium and molar teeth are preserved; in the specimen before us, only the face. The teeth are in such different stages of wear in the two specimens that they may or may not pertain to different species. Almost certainly it cannot be referred to *M. zygomaticus*, from the type of which it differs in its smaller size and less pronouncedly hypsodont dentition.

The incisors, canines and first premolar in the upper jaw are represented only by alveoli, but these show that the canine was rather slender and was followed with hardly an appreciable diastema by p. 1, which was implanted by two distinctly separated fangs, the anterior one of which is considerably larger than the posterior. The second premolar has almost plane external face, with no median ridge and only the faintest trace of a cingulum. The crown is so much abraded that only a small enamel invagination on the inner side of the tooth remains visible. So far as can be judged from its present worn condition, the construction of p. 3 is very much the same as that of p. 2, but with a more prominently developed deutercone. As in the genus, and indeed the family, generally, p. 4 consists of two crescents; a difference from the species of the upper Loup Fork is to be found in the strongly developed internal cingulum.

The molars increase in size from m. 1 to m. 3; they appear to be as brachyodont as in the type specimen, though this may be due, in part at least, to their abraded condition. The external pillars (para- and mesostyles) are less prominent than in *M. zygomaticus*.

The face has not attained that great vertical depth in the region of the orbits which is characteristic of *M. zygomaticus*; the orbit is more oval in shape and more oblique in position than in that species and is notched superiorly; the forehead is more inflated by the sinuses. There are no supraciliary ridges, and the sagittal crest must have commenced at a point considerably farther back than its origin in *Mesoreodon*. The malar is not so heavy as in *M. zygomaticus*, and the masseter ridge is continued well forward upon the maxillary, which displays a slight facial depression above p. 2 and p. 3. The infraorbital foramen is double; the antero-superior foramen is above p. 3 and the postero-inferior opening above the space between p. 3 and p. 4. The lachrymal is large and has an extensive but not very deep depression. A facial vacuity was obviously present between the maxillary, lachrymal and frontal, but its size and shape cannot be determined, as none of the bones mentioned have complete margins and the nasals are entirely lost. The anterior nares are low, very much nar-

rowed inferiorly and expanding into a transverse oval above. The premaxillaries have a high and broad alveolar portion which forms an abruptly truncated muzzle; the two bones are ankylosed at the symphysis. The ascending rami are short and have broad, flattened anterior faces. The palatine processes of the premaxillaries are very limited, while the incisive foramina are quite large and extensively emarginate the palatine plates of the maxillaries. The last-named processes are both long and broad and of nearly uniform width, the two series of teeth diverging but little posteriorly. The palatines are very large and form nearly half of the roof of the mouth. Transversely, they extend almost to the molar alveoli, and anteriorly they are carried as far as the middle of m. 1; they are of uniform width, except behind the molars, where they are constricted by the broad palatine notches. The posterior nares are not indicated in the specimen, but obviously they were placed far back, as the palatines are preserved for some distance behind the last molar.

Measurements.

	M.
Length of molar-premolar series084
Length of premolar series041
Length of <u>p. 2</u>010
Width of <u>p. 2</u>006
Length of <u>p. 3</u>011
Width of <u>p. 3</u>011
Length of <u>p. 4</u>009
Width of <u>p. 4</u>012
Length of true molar series.....	.043
Length of <u>m. 1</u>012
Width of <u>m. 1</u>012
Length of <u>m. 2</u>017
Width of <u>m. 2</u>013
Length of <u>m. 3</u>020
Width of <u>m. 3</u>014

MERYCOCHÆRUS Leidy.

Proceeds. Acad. Nat. Sci. Phila., 1858, p. 24.

The collection contains nothing from the lower Deep River beds which can be confidently referred to this genus, but there can be no doubt that they occur in those beds because of their abundance both in the John Day and in the Loup Fork. On the other hand, the upper strata of the Deep River valley yielded specimens of *Merycochærus* in profusion. Among these specimens there is great variation in size, and other characters as well, so great as apparently to indicate more than one species, but the only one which can be definitely identified is the *M. montanus* Cope.

MERYCOCHÆRUS MONTANUS Cope.

Proceedings Amer. Philos. Soc., Vol. XXI, p. 531.

This species is one of the most abundant and characteristic forms of the upper beds and is represented in the collection by specimens which include nearly all parts of the skeleton, the only important structures which are absent being the scapula and pelvis.

The skull and dentition of this genus are well known, and for this species in particular have been very fully described by Cope. It will suffice, therefore, for our present purpose to give a brief summary of the more characteristic features of these structures, with especial attention paid to the numerous variations displayed by the various specimens.

As in the other members of the genus, the face is bent downward upon the basi-cranial axis and is much more elongate than in the other genera of the family, all of which are characterized by short faces, and in some this shortening is extreme. The brain-case, on the other hand, is relatively short and well rounded. The orbit is small and situated high in the face. The occiput is high and narrow above, though broader than in the other species of the genus in which this region of the skull is known, and becomes very wide at the base. Above the foramen magnum is a narrow but strong median convexity, which is bounded on each side by a deep fossa and which passes superiorly into the shallow concavity which is enclosed between the wing-like processes of the supraoccipital and parietals. The latter processes project much less strongly backward and more transversely than in the older genera of oreodonts or than in the John Day species of *Merycochærus*. The occipital condyles do not project very strongly behind the plane of the paroccipital processes, though in this respect there appears to be considerable individual variation. The foramen magnum is unusually high and narrow. The paroccipital processes are very broad at the base, but long, tapering, slender, and antero-posteriorly compressed in the free portion. The tympanic bullæ are large, especially from before backward, extending anteriorly beyond the line of the postglenoid processes and nearly to that of the glenoid articular surfaces; between the tympanics the basioccipital is narrow and compressed and has a strong inferior keel. The squamosal forms most of the side wall of the cranium and sends off a massive zygomatic process, which, however, is not so heavy as in the John Day species, *M. macrostegus*. The different specimens in the collection exhibit considerable variation in regard to the weight of the zygomatic process, which does not appear to be of a sexual character, for the differences are not correlated with the size of the canine teeth. In the type of *M. montanus*,

"the zygoma as far as the anterior border of the glenoid cavity is slender, and not convex, but flat in every direction, nor is it decurved, as in *M. superbus*. The zygomatic foramen is relatively much smaller than in that species, but is oblique outwards and forwards at an open angle. The obtuse median edge of the zygoma looks upwards, not outwards, as it does in *M. superbus* and *M. macrostegus*, and the superior expansion is opposite the internal extremity of the glenoid face, instead of the external, as in *M. superbus*, or the middle, as in *M. macrostegus*" (Cope, No. 7, p. 531).

None of the specimens in the Princeton collection agree altogether with the type in the construction of this region of the cranium. The description applies best to an almost perfect skull, which, however, differs from the type in the outward and backward direction of the posterior or preglenoid boundary of the "zygomatic foramen." The shape of this opening is different from that seen in the two John Day species which have been mentioned in having its longer axis directed antero-posteriorly, while in them it is transverse. In this specimen the massive and rugose superior expansion of the zygoma is, as in *M. macrostegus*, above the middle of the glenoid cavity, not above its internal edge, as in the type of the species. A second specimen has the long axis of the zygomatic opening transversely directed, as in the John Day species, and the zygomatic process with its superior expansion is almost as heavy and rugose as in *M. macrostegus*. This specimen may perhaps represent another species, but the variation in this region of the skull is so great that species can be distinguished only with difficulty. Other specimens show differences of greater or less degree from the two which have been described, which increases the difficulty of distinguishing species.

The jugal is flattened and beneath the orbit has great vertical depth. The orbits present more laterally and less obliquely forward than in *M. macrostegus*; they are also smaller and less prominent than in that species. The forehead is much narrower than in the John Day form and made more convex by the enlargement of the frontal sinuses and is decurved at the orbits. In *M. macrostegus* this decurvature does not occur; the forehead is very wide and almost perfectly flat. The lachrymal is very large and has a deep pit which is very much better marked than in *M. macrostegus*. The facial portion of the maxillary is shorter but has a greater vertical height. The nasals are very long and project beyond the alveolar border of the premaxillaries, as they apparently do not in *M. macrostegus*; their free ends are obtusely rounded and slightly decurved. They are broader and less decurved at the edges than in the John Day species, but nevertheless are somewhat convex from side to side. The shape of the muzzle is very different in the two species; in the more

ancient form the premaxillaries are very broad, very much depressed and flattened, and the broad surface presents upward; the anterior nares are rather lower, but the narial notch is deeply incised, extending back over p.2. In *M. montanus*, on the other hand, the premaxillaries present their broad surfaces anteriorly, not superiorly, which makes the alveolar less depressed and of greater vertical depth; the narial opening is higher, but does not extend so far back, only a little behind the line of the canine.

The mandible also differs much in the two species. In *M. montanus* the horizontal ramus is somewhat deeper and has not so straight an inferior border; the symphysis is longer, straighter and more inclined, less procumbent and projecting at the incisive alveolus. The angle extends to a much less degree and less abruptly below the inferior border of the horizontal ramus, but, on the other hand, it projects farther behind the plane of the condyle, from which it is separated by a more decided notch. The masseteric fossa is smaller, but deeper and more distinctly demarcated. The coronoid is very peculiar; it is short, broad and blunt at the tip, and projects forward much more than upward, in consequence of which the coronoid notch is very broad and shallow.

The dentition has no very marked peculiarities. In the upper jaw the incisors are very small, with compressed, simple and obtusely pointed crowns; they increase regularly in size from the first to the third. The canines are very large and of the trihedral shape usual in the family. The anterior premolars have crowns which are low but long antero-posteriorly, with trenchant margins; p.4 is less extended in the fore-and-aft direction. The molars increase in size from the first to the third and exhibit little peculiarity of structure. The external buttresses or styles are quite prominent, but the metastyle of m.3, the enlargement of which is so constant a feature in species of *Merycochaerus* as to be of generic value, is smaller than in the John Day species. The para- and mesostyles are prominent, but thin and compressed, and the external faces of the para- and metacones are but slightly concave.

In the lower jaw the incisors are considerably larger than the corresponding upper series and have high, chisel-shaped crowns; that of the median incisor is very narrow; the second is broader and the third still more so. The canine is functionally one of the incisors, but is much larger than any of those teeth and its crown is pointed rather than chisel-shaped, with obliquely descending supero-external border, which is compressed and trenchant.

As in the oreodonts generally, p.1 has assumed the form and function of the canine and is very robust. The crown of p.2 is compressed, trenchant and elongate antero-posteriorly; the deuterocoid is represented by a ridge on the inner face. P.3

is similar, except that the inner ridge is more prominent and encloses a shallow posterior fossette. The fourth premolar has all the elements of a molar, though owing to the small size of some of these elements it cannot be called exactly molariform. The protoconid is crescentic and there is a small paraconid; the postero-external crescent is formed by the metaconid, which is low and obscurely separated from the protoconid; the deutoconid is very clearly demarcated from the protoconid and a low tetartoconid completely encloses the posterior valley or fossette, while the anterior valley still opens internally between the para- and deutoconids. The molars are high and elongate from before backward, and increase in size from $\overline{m. 1}$ to $\overline{m. 3}$; the cingulum is developed only on the front and rear faces of the crown, and a tubercle between the external crescents represents the mesostylid. The talon of $\overline{m. 3}$ is large and consists of two crescents separated by a narrow valley.

The only specimen of a cranial cast in the collection which can be referred to *Merycochaerus* is not in a satisfactory state of preservation and displays but little that is characteristic. Compared with the brain-cast of *Mesoreodon*, it exhibits similar differences to those which are to be observed between larger and smaller species of existing artiodactyls. The hemispheres are broader and of more uniform width, tapering less anteriorly; the convolutions are but obscurely marked in the specimen and can be interpreted only with difficulty, but the sulci appear to be more sinuous and the accessory sulci somewhat better developed than in *Mesoreodon*. The anterior portion of the hemispheres is of greater vertical depth proportionately, while the temporo-sphenoidal lobe is relatively rather smaller. The medulla oblongata is large and of subcircular section. The cerebellum is too much damaged for accurate description, but it appears to be rather high and narrow.

The atlas is broad, short antero-posteriorly and of robust construction. The anterior cotyli are large both vertically and transversely; the two surfaces are almost in contact below, but above are separated by a wide triangular notch which emarginates the neural arch. The neural canal is relatively small, especially its anterior opening. The sides of the neural arch are steeply inclined and end above in a massive tubercle, which forms a spine of unusual height. The articular surfaces for the centrum of the axis form an angle of about 45° with the median line; in shape they are low and wide and their medial edges are reflected upon the sides of the neural canal to form the very large continuous facet for the odontoid process. The inferior arch is strongly convex from side to side and displays a small hypapophysial tubercle near the hinder margin. The transverse process extends well forward and has converted the atlanteo-diapophysial notch into a foramen. The process is not much extended transversely but widens posteriorly; its course on the side of the vertebra is

very obliquely downward and backward, and its antero-external border is thickened and rugose and curved upward in a way that is not found in the other genera of the family; there is no vertebrarterial canal.

The axis is not very well preserved in any of the specimens, but nevertheless some characters of importance may be determined. The centrum is long and depressed, with a prominent inferior keel and slightly concave posterior face. The odontoid process is peculiar; for most of its length it is broad and depressed, with flat superior and convex inferior surface and irregularly semicircular free margin; just before joining the centrum the vertical thickness of the process is suddenly increased, so as to form a step-like elevation on the upper surface along this line. The lateral borders are elevated for a short distance from the centrum, giving the process a spout-shaped section, but at the step already mentioned these raised borders abruptly cease and more than two-thirds of the dorsal face of the process is flat. The neural canal is notably small, with its greatest diameter directed transversely. The neural spine is enlarged into a great plate, which apparently is continued into a posterior spine-like process, as in *Eporeodon*, though this is not altogether certain.

The remaining cervicals have rather short, broad and depressed centra, with opisthocelous and somewhat oblique articular faces; on the ventral side is a prominent keel, which bifurcates behind and into two tubercular ridges, which enclose between them a narrow triangular depression; on each side of the median keel is a deeply concave fossa. The neural canal is very small and of subcircular shape. The neural arch is broad and short and has a nearly flat dorsal surface. The zygapophyses are broad and flat and present nearly vertically and are but slightly oblique in position; the posterior pair considerably exceed the anterior in transverse breadth. The spine forms a low ridge on the third vertebra, but on the fourth it is well marked and becomes longer on the succeeding vertebræ, though it is still very short on the fifth. The transverse processes are variously developed on the different vertebræ; the pleurapophysial plate is very large and massive on the third, and especially so on the fourth, while on the fifth it is smaller and its posterior portion extends outward instead of backward. In all, except the seventh, the vertebrarterial canal is very large. As a whole, the neck of *Merycochærus* was obviously rather short but heavy, as the structure of the vertebræ indicates the presence of massive and powerful muscles.

The thoracic vertebræ are represented by several from different parts of the column, belonging to one individual. In the anterior part of the region they have short, broad and depressed centra, with spines much heavier than usually occur in the oreodonts. Posteriorly, the centra become longer and assume the trihedral form

with slightly opisthocœlous faces which is commonly found among the larger artiodactyls. In the middle and hinder parts of the region the spines become lower and more slender. The transverse processes in the middle region rise high above the centra and project conspicuously outward.

The lumbar vertebræ number at least five, since that many are preserved in one specimen. These vertebræ have long, depressed and arched centra, which are quite sharply contracted in the middle. As in the other vertebral regions, the neural canal is notably small, especially in the vertical diameter. The spines are very thin and compressed, but extended antero-posteriorly, and the transverse processes are long and wide but also very thin and depressed. The zygapophyses are of the usual interlocking character, and, in the anterior region at least, the metapophyses are conspicuous. Little is preserved of the sacrum, but enough to show that the pleurapophyses were massive and apparently confined to the first vertebra. No caudals are represented in any of the specimens.

The ribs are known only from a few fragments. It is obvious, however, that the anterior ribs were broader and more flattened than in the other oreodont genera, in which they are remarkably slender for hoofed animals, though probably *Merychys* should be excepted from this statement.

The humerus is rather short but of massive construction, which is merely an exaggeration of the structure which occurs in the smaller and lighter genera of the family. The head is large, projecting strongly backward, and is very convex in both directions, so as to be of almost hemispherical shape. The external tuberosity is greatly enlarged and extends across the entire anterior face of the bone, and is strongly curved so as to follow the shape of the head; its free border rises steeply towards the inner side and is wider than the base, projecting at both ends, especially internally, where it is drawn out into a massive hook. The inner tuberosity is small and the bicipital groove very deep. The proximal portion of the shaft is compressed, but of great antero-posterior depth; the deltoid ridge is not very prominent, but extends far down the shaft. The distal end of the humerus is broad and the trochlea is characteristically like that of the other oreodont genera, as is especially seen in the broad, low and rounded intercondylar ridge and in the very prominent and massive internal epicondyle.

The ulna is heavy and altogether unreduced, being larger than the radius, except at the distal end. The olecranon is extremely high and deep antero-posteriorly and is thickened and grooved by a tendinal sulcus at the free end. The upper part of the articular surface for the humeral trochlea is broad, but then abruptly contracts and is continued downward only upon the internal side, and the radial facets are distinctly

separated by a rather deep groove. The shaft is strongly arched forward and proximally is broad and trihedral; below, it becomes more and more compressed, and in the middle of its course is of almost rectangular section. The distal end is slightly contracted, both transversely and antero-posteriorly, and is almost concealed from view by the radius when seen from the front. The cuneiform facet is simply convex and has its long axis placed nearly in the fore-and-aft direction. The radius retains the family peculiarities in a very marked degree. The head is not greatly expanded and displays the usual three facets for the humeral trochlea. The shaft becomes more and more slender until the middle of its course is reached and then gradually broadens to the distal end. This form of shaft is highly characteristic of the oreodonts and is in marked contrast to the broad shaft of oval section which is found among the true ruminants. The distal end of the radius is broad, thick and rugose, contracting somewhat suddenly to form the carpal facets; there are no well-marked sulci for the extensor tendons. The surfaces for the scaphoid and lunar are connected in front by a sort of bridge, but for the rest of their extent they are separated by a wide and deep cleft. The scaphoid facet is somewhat oblique in position, is strongly concave from side to side, and is reflected far up upon the postero-internal angle of the bone. The lunar facet is wider and of a saddle shape, being somewhat convex transversely and concave antero-posteriorly.

The carpus of *M. montanus* presents some differences from that of the species from the upper Loup Fork, which I have elsewhere described under the name of *M. cænopus* (No. 32, p. 346). The scaphoid is large in all its dimensions, but compared with that of the true ruminants, its most striking feature is its great vertical height. The radial surface is rather curiously shaped; the anterior ridge is narrow, but the articular surface descends far down upon the anterior face of the bone and the posterior concavity is extended in both directions. The antero-external angle of the proximal end is drawn out into a spur which occupies the "bridge" on the radius mentioned above. The inferior facet for the lunar is very large, both antero-posteriorly and (near the dorsal side) vertically as well; this facet is but slightly concave. The distal surface is very unequally divided between the facets for the trapezoid and magnum, that for the former being of nearly the same dorso-palmar depth, but much narrower transversely than the latter. There is no articular surface for the trapezium.

The lunar is a very curious bone; its radial surface is so warped as to be both convex and concave in both directions; the anterior border rises steeply towards the ulnar side, where it forms a narrow projection for the cuneiform. The proximal contact of the two bones is limited to this small facet, and behind it the upper portion of the lunar is much contracted. On the radial side there is no superior facet for the

scaphoid, but the inferior one is very large and passes without interruption into the surface for the magnum, which is altogether lateral in position. In *M. cænopus* the magnum facet is strongly convex, but in *M. montanus* it is almost flat. The lunar rests entirely upon the unciform and its whole distal surface is occupied by the large concave facet for that bone; it is very oblique in position and forms, with the magnum surface, a sharp edge or beak which descends almost to the third metacarpal and prevents any anterior contact between the magnum and unciform.

The cuneiform has an oblique position in the carpus, running outward and backward from the lunar. In shape it is rather low and narrow, but greatly extended in the dorso-palmar direction. The radial side presents two facets for the lunar, of which the proximal one is very small and the distal one quite large. The proximal surface for the ulna is a simple groove and the facet for the pisiform is large, triangular and almost flat. The distal face of the bone is occupied by the large and simply concave surface for the unciform.

The trapezium is preserved in Prof. Cope's type specimen and, as in the case of *Mesoreodon*, demonstrates that the pollex was not present. It is a small nodular bone which appears not to touch the scaphoid but to articulate merely with the trapezoid and second metacarpal.

When seen in position, the trapezoid appears to be as large as the magnum, but is really very much smaller in all its dimensions. The proximal side forms a narrow, imperfectly saddle-shaped facet for the scaphoid, and on the palmar side is a small surface for the attachment of the trapezium; on the ulnar side the trapezoid is closely applied to the magnum. The metacarpal facets are two in number, a large distal one for the second and a small infero-lateral one for the third metacarpal.

The exposed anterior face of the magnum is quite small and yet the bone is a rather large one. The proximal surface is altogether taken up by the facet for the scaphoid, the contact with the lunar being entirely lateral. The scaphoid surface is very convex and rises steeply towards the palmar side to form an ill-defined head. The lunar facet is but slightly concave and in this respect is very different from the surface which occurs in *M. cænopus*, where the magnum encloses the lunar almost in a semicircle. On the radial side of the magnum is quite a deep concavity which receives the trapezoid. The hook-like process which is given off from the palmar side of the magnum is long and heavy and is strongly recurved towards the radial side. The distal side bears a saddle-shaped facet for the third metacarpal, but there is no anterior contact with the second.

The unciform is a large bone of irregularly cuboidal shape. The proximal surface is almost equally divided between the facets for the cuneiform and lunar, though

the latter is somewhat smaller and much more oblique in position, being almost as much lateral as proximal and continuing without interruption into the facet for the third metacarpal, which is relatively large. The distal side bears facets for the fourth and fifth metacarpals, of which the latter is unusually large. The posterior hook of the unciform is long and heavy and projects downward and backward, but is not curved laterally.

In *Merycochoerus* the metapodials attain a degree of shortness and heaviness such as is found in no other genus of the family, and the lateral digits in particular are relatively very stout, so as to recall in some degree the feet of the hippopotamus. The second metacarpal is short and heavy, with a small head, which bears a narrow convex head for the trapezoid and on the postero-external side a small facet for the magnum. There is no anterior contact with the magnum, this bone being excluded from the second metacarpal by the extension of the third to the trapezoid. On the postero-external angle of the head is a small facet for the trapezium. The shaft is somewhat contracted in the middle and is broadest just above the distal trochlea, which is very unsymmetrical in shape. In *M. cænopus* the second metacarpal is decidedly more slender and compressed than in the species before us.

The third metacarpal is much the stoutest bone of the series and its shaft is of almost uniform breadth throughout, though slightly expanding towards the distal end. The head bears a large number of facets and is very completely and perfectly interlocked with the surrounding bones. On the radial side is a flat, horseshoe-shaped surface for the second metacarpal, and above this a small, triangular facet for the trapezoid, which surface, however, is confined to the dorsal moiety of the bone, dying away towards the palmar side and allowing the second metacarpal to reach the magnum. The magnum facet is deeply concave from side to side and convex from before backward; the antero-external angle is drawn out into a heavy process, which overlaps the head of mc. iv and abuts against the unciform. The posterior facet for the fourth metacarpal is large and somewhat oblique, so as to extend slightly underneath that bone. The distal trochlea is low and broad; its carina is very prominent but does not extend upon the dorsal side.

The fourth metacarpal is of about the same length as the third and the shaft has the same antero-posteriorly compressed shape, though it is not so wide transversely. Although the fourth metacarpal is actually no longer than the third, it extends beyond it distally, for the third rises higher at the proximal end. In *Oreodon*, mc. iii considerably exceeds mc. iv in length and projects beyond it both proximally and distally. The surface for the unciform is not very broad and towards the palmar side it becomes obliquely lateral in position. The fifth metacarpal is somewhat

shorter than the second and is heavier, especially towards the distal end; the facet for mc. iv is oblique in position. While the median metacarpals are closely applied to and run parallel with each other, the lateral ones, mc. ii and mc. v, diverge quite strongly from the median axis, and thus give a foot with a very broad base.

The phalanges are short, broad, much depressed and flattened. Unguals are not preserved in any of the specimens.

Except for its increase in size and weight, the femur differs but little from that of the older genera of the family. Compared with the femur of *Eporeodon*, the following changes may be observed. The head is rather more sessile and projects more upward and forward and the pit for the round ligament is larger and deeper. The neck is less constricted and the bridge connecting the head with the great trochanter is thicker and more rugose. The great trochanter, though massive and extended antero-posteriorly, is rather low, not rising so high as the head; it encloses a very deep digital fossa. The second trochanter is smaller and less prominent. The shaft is broader and less rounded and the medullary cavity is larger, with thinner walls. The deep pit above the external condyle for the origin of the plantaris muscle is more conspicuously marked. As in the John Day genus, the condyles are of nearly equal size and are separated by a wide and deep groove. The rotular trochlea is somewhat more modernized, being wider and less symmetrical; the external border is more prominent and continued farther distally than the internal.

The proximal end of the tibia is not known. The distal end is very heavy; the external fossa for the astragalus is considerably broader and less deeply incised than the internal one, and the malleolar process is remarkably long and heavy; on the external side is a small concave facet for the fibula. The fibula has a shaft which is very large in the antero-posterior dimension, though very thin and compressed laterally. In the upper Loup Fork species, *M. cænopus*, the shaft is much more slender and reduced to almost thread-like proportions. The distal end is expanded into a very heavy external malleolus, which, like the shaft, has its greatest diameter antero-posteriorly. On the inner side is a projection which fits into a groove on the tibia, and distal to this is a large plane surface for the astragalus, which does not, however, occupy all of the tibial side of the malleolus. The calcaneal facet is narrow and slightly concave transversely, but extended in the fore-and-aft direction.

The tarsus is lower and broader and the individual elements more massive than in the earlier genera of the *Oreodontidae*, but otherwise there is little change. The astragalus is low and broad; the external proximal condyle is considerably larger than the internal, but the difference is less extreme and the intercondylar groove is narrower and deeper than in *M. cænopus*. On the distal trochlea the navicular sur-

face is wider and the cuboidal narrower than in the last named species. The calcaneum is short and massive and is remarkable for the sessile character of the sustentaculum; in the other members of the *Oreodontidæ* the sustentaculum projects but very little beyond the tuber, though in none of them, except *Merychys*, is this so marked as in *Merychochaerus*. The fibular facet is elongate antero-posteriorly, narrow and arched. The navicular is relatively wider than in *M. cænopus*, but is so nearly like that of the older well-known genera as to require no detailed description. The cuboid is low and broad and differs from that of *Oreodon* in the relative width of the proximal facets, the astragalar being wider than the calcaneal, while in the White River genus the calcaneal is the broader. The difference in *M. montanus* is not, however, so marked as in the species from the upper Loup Fork. The calcaneal facet is not only narrower than in *Oreodon* but of different shape, the external border being straight and not projecting beyond the body of the bone. The facet for the astragalus is not so deeply concave as in the more ancient genera of the family, the dorsal and plantar margins not rising so high. On the tibial side are two facets for the navicular, which are separated by a deeper sulcus than in *Oreodon*. The distal side is almost completely taken up by the large facet for the fourth metatarsal; that for mt. v is very small and rather lateral than distal, while in *Oreodon* it is altogether distal. The posterior hook of the cuboid is very massive.

The entocuneiform is quite a large nodular bone, which articulates with the navicular and mesocuneiform and abuts against the plantar side of the head of the second metatarsal, which it holds firmly in place. As in all the known members of the *Oreodontidæ*, the meso- and ectocuneiforms are coössified, and, since the former has less vertical height than the latter, the compound bone appears to have a step cut in its distal side, which receives the head of the second metatarsal and prevents the third from reaching the mesocuneiform.

The metatarsus departs less from the family type than does the metacarpus, both in its proportions and in its mode of articulation with the podials. The median metatarsals are, however, relatively shorter and more massive and the laterals more reduced than in the more ancient genera. The slenderness of the laterals and their parallelism with the medials are in striking contrast to the lateral metacarpals, which, though shorter than the median pair, are nearly as heavy, and which diverge strongly from the axis of the manus. The second metatarsal is not only proportionately, but even actually, shorter than in the much smaller *Oreodon Culbertsoni*, and is the shortest of the series. The head articulates with all three of the cuneiforms; on the posterior side is a facet for the entocuneiform, the proximal end is supported by the mesocuneiform, and since the latter is of less height than the ectocuneiform, the fibular side

of the head of the metatarsal is in contact with the ectocuneiform element of the compound bone. The shaft has considerable dorso-plantar diameter, but is very much compressed laterally, and therefore, when seen from the front, appears to be exceedingly slender. The third metatarsal is considerably longer than the second, though relatively very much shorter than in the other genera of the family, and is very massive. The proximal facet is almost plane and articulates only with the ectocuneiform; a process on the fibular side slightly overlaps mt. iv, but appears not to reach the cuboid; if it does, the contact is very slight. The fourth metatarsal is somewhat longer and rather heavier than the third, and by its broad, plane proximal surface occupies nearly the entire distal side of the cuboid. The fifth metatarsal is somewhat longer and not so compressed and slender as the second; its contact with the cuboid is small and rather lateral than distal.

The phalanges do not differ in any important respect from those of the manus; they are somewhat longer and narrower, and those of the lateral digits are smaller. In particular, the unguals of these digits are very small.

CYCLOPIDIUS Cope.

Proceedings Amer. Philos. Soc., Vol. XVII, p. 221.

The distinction of this genus from *Leptauchenia* is an obscure one. Cope defines *Cyclopidius* in brief as being "*Leptauchenia* without superior incisor teeth;" but this character appears not to be altogether constant, for some specimens show a small alveolus in each premaxillary, and others, described below, have two minute upper incisors on each side. All the peculiarities of *Leptauchenia* are exaggerated in this genus. The lower incisors are reduced to two in each ramus. The upper canine is usually very small and extends but little below the level of the premolars; the latter, especially the two anterior ones (p.1 and p.2), are, in the typical species, reduced in size and simplified, but none are lost. The molars are more prismatic than in *Leptauchenia*, and in the upper series the external pillars or styles are more prominent. The first lower premolar retains the form and function of the canine, but is only slightly larger than in the canine proper. The facial region of the skull is much shortened and the vacuities enlarged; the brain-case is small and narrow, but the great expansion of the roots of the zygomatic processes makes the cranial region very broad and low. The auditory meatus is very long and its opening has a more elevated position than in *Leptauchenia*. The frontal zone is very short and the frontals form but little of the cranial roof. The nasals are short and slender rods, expanding somewhat anteriorly, where they meet the ascending processes of the maxillaries and premaxillaries; the latter are very small.

CYCLOPIDIUS INCISIVUS Scott.

Amer. Naturalist, 1893, p. 661.

This species might with almost equal propriety be referred to *Leptauchenia*, since it is, in many respects, a connecting link between the two genera; it is much like *C. simus*, on the one hand, and *L. decora* of the White River beds on the other. It differs from the latter species principally in the much more reduced incisor teeth and in the larger premolars, and from the former in the presence of two incisors in the premaxillary, the larger upper canine and premolar teeth and in details of skull construction. As in all the species of *Leptauchenia*, the infraorbital foramen is very small and placed above p. 3. The upper incisors, two in number, are extremely small, especially the median one, which is hardly more than a rudiment; the second incisor is almost twice the width of the first and has an obliquely truncate cutting edge. The two incisors of each side are implanted very close together, the first somewhat overlapping the second, while a considerable gap separates the median pair. The canine is larger than in the typical species of the genus, though this character may be sexual, and is followed by a short though distinct diastema, which about equals the fore-and-aft diameter of the canine. The premolars increase in size posteriorly. The first is very small and simple; p. 2 has a low internal ridge representing the deuterocone, which in p. 3 becomes very distinct and is connected by a ridge with the postero-external angle of the crown, the valley opening in front. The first three premolars have convex external faces, and are so inserted as to project slightly backward as well as downward. The molars increase in antero-posterior diameter from the first to the third, m. 3 markedly exceeding m. 2 in this dimension, as the latter exceeds m. 1; in transverse width, however, m. 3 is the least of the series and has much the highest crown.

The nasals are more expanded anteriorly at their junction with the maxillaries than even in *Leptauchenia decora*. The nasal opening is terminal, presenting anteriorly, and is of heart-like shape, with the apex downward. The premaxillæ are of somewhat peculiar form; the alveolar portion is insignificant, but the ascending rami form quite a high symphysis and present their broad surfaces anteriorly, while the superior expansions are twisted, so as to present laterally. The palate is long, broad, and concave from side to side, the two molar series being almost parallel, while the premolars converge anteriorly. The palate is carried farther behind the last molar than in *L. decora* and, compared with that species, the posterior nares have been shifted backward. The incisive foramina are very small and anterior in position.

Measurements.

	M.
Length of molar-premolar series.....	.064
Length of premolar series.....	.029
P. 1, length.....	.005
P. 1, width.....	.004
P. 2, length.....	.007
P. 2, width.....	.005
P. 3, length.....	.008
P. 3, width.....	.006
P. 4, length.....	.007
P. 4, width.....	.007
Length of molar series.....	.037
M. 1, length.....	.009
M. 1, width.....	.010
M. 2, length.....	.013
M. 2, width.....	.010
M. 3, length.....	.015
M. 3, width.....	.009

The type of this species was found by Mr. R. Stevenson in the upper beds.

PITHECISTES Cope.

Proceedings Amer. Philos. Soc., Vol. XVII, p. 219.

In this genus, which is as yet very imperfectly known, the *Leptauchenia* series of oreodonts appears to have reached its culmination. The lower incisors are reduced to one, the canine has resumed its original functions, and the caniniform premolar has disappeared. The other premolars are greatly reduced in size and the mandible is extremely shortened in consequence.

Found only in the upper beds of the Deep River valley.

MUTUAL RELATIONS OF THE OREODONT GENERA.

In my paper upon this family (No. 32), lack of material compelled me to leave many questions with regard to the mutual relations of its genera unsolved and even unattempted. The newly discovered material will enable us to answer some of these questions with a reasonable degree of probability. We may first consider the origin of *Merychyus*.

The relationship of *Mescreodon* to the typical *Eporeodons* of the Oregon John Day is very obvious and need not be dwelt upon, the only difference of taxonomic value between the two genera being in the structure of the manus, and indeed there is much to be said in favor of giving *Mesoreodon* only subgeneric rank. Nevertheless, in the skull and, to a less degree, in the dentition, we may observe numbers of

slight and subtle changes which are all in the direction of *Merychys*. If such species of the latter genus as *M. zygomaticus* and *M. pariogonus* be taken into account, the transition from *Mesoreodon* is seen not to be very great or abrupt, though as regards dentition and skull structure there still remains a considerable gap between the two genera, which is only one of the many signs that point to a hiatus between the lower and upper beds of the Deep River deposits. In the *Merychys* species from the lower Loup Fork (upper Deep River), *M. zygomaticus* and *M. pariogonus*, the face has become deeper and the cranium shorter and the wing-like posterior processes of the parietals are reduced; the nasals are shortened and a fontanelle is formed between the frontal, lachrymal and maxillary. The premaxillaries are depressed, flattened, and ankylosed at the symphysis. In foot structure, *Mesoreodon* has already attained the condition of *Merychys*, especially if the more slender and elongate foot of *M. intermedius* be regarded. In the dentition the principal change consists in a modification of the premolars and a rearrangement of the adjacent horns of the internal crescents on the upper molars, for *Merychys pariogonus* shows that the hypsodont molars have been acquired within the limits of the genus. We may, therefore, provisionally at least, regard *Mesoreodon* as ancestral to *Merychys*, and the line of descent would then be: *Oreodon*—*Eporeodon*—*Mesoreodon*—*Merychys*.

If this view of the case be correct, then the relationship of *Merychys* to *Merycochoerus* must be strictly one of parallelism, by which the articulation of the third metacarpal with the trapezoid and the depressed and ankylosed premaxillaries have been independently attained in the two genera. *Merychys* has also run parallel to *Leptauchenia* in the development of facial vacuities and in the disposition of the crescents of the upper molars as well as their hypsodont character. Yet, now that we know the skull structure of these two genera, no one could seriously maintain that they are genetically connected, though Leidy's suggestion of such connection was natural enough from the material at his command. To unite *Merychys* and *Merycochoerus* into a single genus, as Leidy proposed in his later work (No. 24, p. 201), a suggestion which Bettany adopted (No. 1, p. 262), would be to construct an unnatural polyphyletic group, unless genera are to be artificial assemblages united only by certain common characters, the morphological value of which is unimportant. It must be remembered that *Merycochoerus* is a much older form than *Merychys*, its peculiarities having all been established in the John Day. To derive the latter genus from the former, it would be necessary to make some highly improbable assumptions. (1) We should have to assume that the face had become depressed upon the basi-cranial axis, only to again straighten out and lie in a line with that axis. (2) That the face, after having elongated more than in any other genus of the family, had

once more become shortened. (3) That the orbit, after retreating backward so as to be almost entirely behind the line of the molar teeth, had again advanced over those teeth. (4) That the zygomatic arches, after having attained an extraordinary degree of size, massiveness and rugosity, had dwindled to proportions even smaller and lighter than those of *Oreodon*. (5) That the posterior nares had first been pushed back to a remarkable extent, and had again resumed their original position. (6) That the metapodials, after becoming short and massive to a very unusual extent, had attained a degree of length and slenderness which is equally unusual in this family.

We have, it is true, already found reason to believe that, in the horses, progress in the main is accompanied by a certain amount of oscillation in the minor details of structure and that even a certain degree of specialization in a direction away from that taken by the phylum as a whole, may be overcome and suppressed, as, for example, in the case of the elbow joint of *Meshippus*. Nevertheless, we know of no facts which would justify us in assuming oscillations of such amount as would be involved in the derivation of *Merychius* from *Merychochærus*. If we reject *Mesoreodon* from the ancestry of the former genus, then we must admit parallelism in the structure of its manus, and thus, whichever horn of the dilemma be accepted, the fact that "adaptive" reduction of the manus has occurred twice independently within the limits of the family cannot be avoided, for to regard *Mesoreodon* as in any way descended from *Merychochærus* is a manifest absurdity. The simplest and most probable conclusion is therefore that *Merychius* and *Merychochærus* represent two independent branches of the oreodont stem, which in some respects have paralleled each other, the former not attaining until the Loup Fork the structures which the latter had already developed in the John Day.

Recent discoveries have also thrown some light upon the relationships of the *Leptauchenia* series. Leidy ascribed that genus to the White River formation, while Cope believed that it was confined to the Deep River beds, though it had not been found in the typical (Montana) locality of that horizon. In my former paper I followed Cope's determination, chiefly on the ground that no member of this series has ever been obtained in the John Day beds. It is now proven, however, that Leidy's determination is the correct one. Dr. Wortman informs me that he has found *Leptauchenia* in the upper White River beds, and during the past summer (1893) the Princeton party found them in great numbers at the same locality. The morphological difficulty, that all three members of the *Leptauchenia* series were found only in the same horizon is thus removed, but we are still in the dark with regard to the ancestry of this line, which must be sought for in the lower White River beds. We may, however, confidently remove it from all connection with *Merychius*.

Fam. Indet.

HYPERTRAGULUS CALCARATUS Cope.

Bull. U. S. Geol. and Geogr. Surv., No. 1, 1874, p. 26.

A mandible, which is indistinguishable from that of the species named, was found in the lower beds of the Deep River valley, and some specimens from the upper, or Loup Fork, beds of the same locality seem to indicate that the same or a closely allied genus was continued up into the latter series, but the specimens are too fragmentary for certain reference.

BLASTOMERYX Cope.

U. S. Geogr. Surv. W. of 100th Mer., Vol. IV, Pl. II, p. 350.

The status of this genus is very obscure and uncertain. The name was originally applied to $\overline{m. 3}$ of a small animal from the upper Loup Fork of Colorado and New Mexico, which appears to be very much like *Cosoryx*, differing from the latter in the shortness of the molar crowns and better development of the basal pillar. So very little is known of the dentition of this animal that its relationships are quite indeterminate beyond the obvious fact of its alliance with *Cosoryx*. The much larger and more robust species from the lower Loup Fork or Deep River, which has been referred to this genus, not improbably represents a very different one, but materials are lacking for an exact comparison. This Deep River species is in many ways similar to the larger species of *Palæomeryx* from the upper Miocene of Europe, and perhaps should be referred to that genus, though in the present state of knowledge it would be premature to do so. This doubt is justified by the fact that the mandibular dentition of *B. borealis* is still unknown, and we cannot therefore determine whether the lower molars possessed the very characteristic "Palæomeryx fold," and it is uncertain whether the type of the European species had developed horns. Schlosser does not regard the presence or absence of horns as a character of generic value, but with this view I am unable to agree. Further, the character of the horns and the shape of the occiput are different from anything which has been observed in the European types. For these reasons, the name *Blastomeryx* may be provisionally retained. However, by whatever name we call it, there can be little doubt this genus represents a more or less modified migrant from the Old World, not only because of its close similarity, or even identity, with some of the genera of that region, but also because it represents a new element in the American fauna, no form being known from the White River or John Day formations from which it could be derived. That an interchange of mammals between the two continents took place at some time

subsequent to the John Day and before the beginning of the Loup Fork is made evident by such types as *Anchitherium*, *Blastomeryx* and *Mastodon*.

BLASTOMERYX BOREALIS Cope.

Proceedings Amer. Philos. Soc., Vol. XVII, p. 222.

This species is quite a large one, though somewhat smaller than the *Palæomeryx magnus* and *P. sansaniensis* of Sansan. The skull is remarkable for the high and narrow occiput, the upper portion of which is drawn out into a long, backwardly projecting process composed of the parietals and supraoccipital, which is very similar to the corresponding part of the occiput in the *Oreodontidæ*. The horns are trihedral at the base, gradually becoming rounded distally, and are of remarkable length; they are perfectly simple and unbranched, and in no specimen which I have seen is there any trace of a burr. The surface of the horns is faintly marked by vascular impressions, but is on the whole remarkably smooth, much more so than in the antlers of the deer, and, as Cope has suggested, they were doubtless covered with skin throughout the lifetime of the animal. "At the base of the horn on each side a wing-like expansion extends outward posterior to the orbit" (Cope). The upper premolars, three in number, have the internal crescent or deutercone complete; p.2 and p.3 are massive and oval in section, while p.4 is more extended transversely. The molars are very brachyodont and are covered with very rugose and strongly wrinkled enamel; the internal crescents are complicated by accessory spurs, which invade the valleys. The internal pillar or style is very variable, being sometimes quite large, while in many specimens it is absent from one or other of the molars.

BLASTOMERYX ANTILOPINUS Scott.

Amer. Naturalist, 1893, p. 662.

The type of this species is represented by a mutilated skull, three cervical vertebræ and various bones of the fore and hind limbs. It differs from the foregoing species principally in size, being decidedly smaller; the median ribs of the external crescents on the upper molars are less prominent. Other differences are to be observed, but they are perhaps rather apparent than real and due to the imperfect condition of the specimen. The muzzle is broken away, not only in this, but in all known specimens of *B. borealis* as well, and hence nothing is known as to the presence or absence of the upper canine. No isolated teeth have as yet been found in the Deep River beds which can be regarded as the upper canines of *Blastomeryx*, and Filhol reports the same fact with regard to the *Palæomeryx* of Sansan (No. 13, p. 251). On the other hand, Fraas (No. 16, p. 38) refers the muntjak-like canines

which he obtained at Steinheim to the species of *Palæomeryx* occurring at that locality.

In the type specimen of *B. antilopinus* all the premolars are more or less injured; p.1 appears to be altogether absent; p.2 is represented only by the fangs, but enough remains of p.3 and p.4 to show that they differ only in size from those of *B. borealis*. Compared with the corresponding teeth of such European species as *Palæomeryx magnus* and *P. sansaniensis*, these premolars are distinguished by the better development of the deutercone, the narrower valleys and the character of the cingulum, which is but faintly marked on p.4 and absent from p.3. The latter tooth is the largest of the series, exceeding p.4 not only in antero-posterior but also in transverse diameter. The molars increase progressively in size from the first to the third, and in all the transverse width is but slightly less than the antero-posterior length, and the cingulum is confined to the front face of the antero-internal crescent. The anterior and median external pillars (para- and mesostyles) are prominent. The median rib on the outer face of the antero-external crescent is also conspicuous, though on m.1 this ridge is less prominent than in *B. borealis*; the rib of the postero-external crescent is almost obsolete. The internal pillar increases in size from m.1 to m.3, being much larger on m.3 than on either of the other molars; in *B. borealis* this pillar is very small or absent on m.3 and larger on m.1 and m.2. The internal crescents of the molars are much like those of *B. borealis*; the anterior one is less complete than the posterior, its hinder horn being especially shortened; on m.3 the adjacent horns of the two internal crescents are curiously crenulate, in a way that recalls the transverse crests on the upper molars of some of the extinct horses. In *B. borealis* this does not appear to be the case. The upper molars of the Sansan species differ from those of the Montana forms principally in the much better developed cingulum, which embraces the entire crown of the tooth except on its outer side, and in the less developed internal pillar, which is hardly more than indicated in Filhol's figures. The inner crescents are not crenulate and are less complicated by spurs which invade the valleys, and the valleys themselves are more widely open. The *P. furcatus* from Steinheim which Fraas has figured (No. 16, Pl. VIII, Fig. 9) is more like the American species in regard to the structure of the upper molars, so far as can be judged from the drawings. This species is also of interest as showing a mode of formation of the internal crescent of p.2, which I have elsewhere shown to be characteristic of *Procamelus* (No. 34, p. 436), viz, by the coalescence of two distinct ridges in the median transverse line, instead of what is much more usual in the Artiodactyla and universal in the case of p.4, by the extension of ridges from the internal cusp or deutercone.

Measurements.

	M.
Length of premolar-molar series.....	.079
Length of premolar series.....	.037
P. 2, length.....	.013
P. 3, length.....	.013
P. 4, length.....	.011
Length of molar series.....	.043
M. 1, length.....	.014
M. 1, width.....	.013
M. 2, length.....	.016
M. 2, width.....	.015
M. 3, length.....	.017
M. 3, width.....	.016

N. B.—It will be observed that the length of the molar series is less than the sum of the lengths of the individual teeth. This is due to the slight overlapping of the successive molars.

The general aspect of the skull (Pl. VI, Fig. 48) is quite similar to that of *Antilocapra*, though there are many important differences, which, as would naturally be expected, are in the direction of more primitive conditions. The cranium is very long and the face relatively short, as compared with that of most recent ruminants, though long in proportion to the more ancient forms of the group. In correspondence with this, the orbit is placed quite far forward, its anterior rim extending almost to a line above m. 2, and the zygomatic arch is decidedly longer than in the prong-buck. The upper contour of the skull is almost straight, there being hardly any descent at the forehead and little arching of the cranium. In some respects the skull of *Blastomeryx* is more modernized than that of existing hornless deer, such as *Hydropotes* and *Moschus*, especially in the backward shifting of the orbit. In *Hydropotes* the orbit is almost entirely over the molars and in *Moschus* its front border extends nearly as far as the posterior border of m. 1. In both genera, and especially in *Moschus*, the orbit is raised much higher above the molar alveolus than in *Blastomeryx*. On the other hand, the recent genera have a proportionately shorter and more rounded and capacious cranium, the upper contour of which is much more decidedly arched from before backward, and the occiput is lower and without wing-like extensions of the parietals. The paroccipital processes are not advanced in front of the occipital condyles; the zygomatic arch is much shorter and the glenoid cavity more elevated above the plane of the molars, indicating a higher ascending ramus of the mandible.

The specimens do not indicate that in *Blastomeryx* the face was bent down the basicranial axis, as in the recent Cavicornia and some other artiodactyls, but appears rather to have been in the same line with it. The occiput is very broad at the base;

in the median line, above the foramen magnum, is a wide convexity bounded on each side by a shallow fossa. Towards the summit of the inion this convexity passes into a shallow concavity with a faint median keel, inclosed between processes of the supraoccipitals and parietals. These processes are broken away in the specimen, so that their length cannot be determined. Apparently, however, they were not so long and prominent as in *B. borealis*, in which the occiput is utterly unlike that of any existing ruminant and has more the peculiar shape characteristic of the *Oreodontidæ*. Neither Filhol nor Fraas give figures of this region of the skull in *Palæomeryx*, but *Dicroceros* has an entirely different occiput (see Filhol, No. 13, Pl. XXXIV, Fig. 4) which is broad and low and forms a nearly vertical plane.

The paroccipital processes in *Blastomeryx* are long, laterally compressed, and broad at the bases, which are closely applied to the tympanic bullæ. Between the condyle and the paroccipital process the inferior surface of the exoccipital displays a large, deep fossa, which is much larger and more deeply impressed than in *Antilocapra*, and the process stands much more in advance of the condyle than in that animal. The mastoid is exposed upon the surface of the skull and forms quite an area between the squamosal and exoccipital; its lower end forms a dense rugose mass, though there is no proper mastoid process. The relations of the mastoid are very much the same as in the prong-buck, except that it is more advanced in front of the condyle in position and descends lower upon the paroccipital process. The cranium is long and quite full and rounded, though more slender and less capacious than in *Dicroceros*. The parietal zone is very long and roofs nearly the entire cranial cavity; obscurely marked temporal ridges pass backward from the bases of the horns and converge to form a low but distinct sagittal crest, which is longer than in the European genus. The postorbital constriction is not strongly marked, though much more so than in the existing genera of horned ruminants. The squamosal is very large and makes up nearly the whole side wall of the cranium; the root of the zygomatic process forms a thin, depressed plate, which is much extended in the antero-posterior direction and is pierced by a large venous foramen. The zygomatic arch is slender and depressed, and though the distance from the postglenoid process to the last upper molar is nearly the same as in *Antilocapra*, yet, owing to the more anterior position of the orbit, the zygomatic arch is considerably longer than in the modern genus. The glenoid cavity is thoroughly ruminant in character, though the anterior convexity and posterior concavity are more decided and the postglenoid process somewhat longer than in the prong-buck. The tympanic bullæ are small and of the shape usual in the antelopes, with a deep groove for the attachment of

the hyoid apparatus, a feature which is cervine rather than antelopeine; the auditory meatus is a long tube which is directed more posteriorly than in *Antilocapra*.

The frontal zone extends considerably in front of the orbits, though but little behind them, and hence takes but a small part in roofing the brain-chamber; these bones lie in nearly the same plane throughout their length, and the descent at the forehead is slight, very much less than in the prong-buck and apparently less than in *Dicroceros*. Apart from the horns, the upper contour of the skull is thus almost a straight line. The horns are very peculiar and quite unlike those of any other known genus, fossil or recent. At the base the section forms a spherical triangle, the three sides of which present forward, backward and inward; the anterior face is concave, a feature which is much more marked in this species than in *B. borealis*; the other faces are convex. In the specimen before us the horns are broken away about three inches above the base, but Prof. Cope's numerous skulls of the larger species show that in that form, at least, the horns were remarkably long, perfectly simple and non-deciduous, none of them exhibiting any burr or any tendency to branch. The young stages of *Dicroceros* have a very similar unbranched horn, but the many known skulls of *Blastomeryx* show that this simplicity is not a transitory character in this genus (see Filhol, No. 13, Pl. XXXIV, Fig. 3). Faintly marked grooves and ridges may be seen on the surface of the horns, but their smoothness indicates, with great probability, that they were permanently covered with skin. The external angle of the base of the horn is in *B. borealis* continued into a wing-like process which extends outward behind the orbit. In the type of *B. antilopinus* this process is broken away, but it can hardly have been so prominent as in the larger species. As in *Dicroceros* and *Antilocapra*, the horns rise directly above the orbits, but are more erect than in the former genus; the postorbital process is given off from the base of the horn. A large foramen, the supraorbital, pierces the base of the horn and two smaller ones perforate the frontal in advance of the latter; these foramina have a more anterior position than in the prong-buck.

Between the frontal and the lachrymal there is a narrow, slit-like fontanelle, the incipient stage of the much larger vacuity which occurs in the deer and many antelopes. Cope's figure of *B. borealis* (No. 7, Fig. 16) does not show this vacuity; if it be really absent in that species it will form an important specific distinction. The nasals, premaxillaries, and most of the maxillaries are destroyed, but enough of the latter remains to show that the alveolar portion is very low in correspondence with the extremely brachyodont character of the dentition and that the facial portion is high. In consequence of this, the face is deep vertically, quite as much so as the cranium, and the line from the molars to the occipital condyle is straight and nearly

parallel with the straight upper surface of the skull. There is no trace of a lachrymal pit in front of the orbit. In *B. borealis*, and doubtless in the present species also, the maxillaries are sharply constricted in front of the premolars. The infra-orbital foramen occupies a slightly less advanced position than in *Moschus*, opening above the internal between p. 2 and p. 3, while in the existing genus it is over the middle of p. 2. The palate is broad and gently arched from side to side; between the molars it is of nearly uniform width, but it narrows anteriorly, the two premolar series converging slightly forward. The posterior nares extend to about the middle of m. 3 and are very long from before backward, in correspondence with the length of the cranium and zygomatic arches. As contrasted with the base of the skull in *Antilocapra*, the principal difference to be observed is the elongation of the posterior portion, especially the region between the occipital condyles and paroccipital processes, which points to a greater development of the cerebellum and medulla oblongata and is very usual in the crania of primitive mammals. The orbit is also much lower down and farther forward in the face, its upper border not projecting above the superior contour of the cranium.

Nothing is known of the mandible in either species, except some uncharacteristic fragments.

From the foregoing description it will be at once evident that while the skull of *Blastomeryx* is in many respects more primitive than that of any of the recent Pecora, yet it is manifestly of that type and, in some details, such as the character of the occiput and the wing-like processes from the bases of the horns, the genus is specialized in a way peculiar to itself and which renders it somewhat doubtful whether any existing form is to be derived from it.

Measurements.

	BLASTOMERYX ANTILOPINUS.	ANTILOCAPRA AMERICANA.
	M.	M.
Width of occiput at foramen magnum.....	.078	.079
Distance from crest ofinion to middle of horn.....	.104	.085
Antero-posterior diameter of horn base.....	.036	.041
Transverse diameter of horn base.....	.046	.024
Depth of face at <u>m. 3</u>067	.070
Distance from foramen magnum to postglenoid process.....	.051	.045
Distance from postglenoid process to <u>m. 3</u>073	.069
Width of palate at <u>m. 3</u>036	.052

The vertebral column is represented by the second, third and fourth cervical vertebrae. The axis is completely modernized in character and differs only in details from that of *Cervus* or *Antilocapra*. The centrum is broad anteriorly, where it

expands to form the atlanteal surface; behind this it contracts, to expand again slightly towards the posterior end; the hinder face is concave and there is a strongly marked hypapophysial keel. The articular surface for the atlas does not rise quite so high upon the sides of the neural canal as in *Cervus*; its inferior border is more curved and the median notch more deeply cut. The neural canal is lower and broader anteriorly, posteriorly its opening is notably small; the pedicels of the neural arch are perforated for the second pair of spinal nerves, but the foramina are smaller than in *Cervus*; in its anterior portion the neural arch is thin and plate-like, but gradually thickens until, at the level of the postzygapophyses, it becomes massive and diploëtic. The spine is so broken that its shape cannot be determined, but it appears to have been thicker and heavier than in *Cervus elaphus*. The transverse processes are also broken away, but it can be seen that they were slender and probably short. The odontoid process is completely spout-shaped but has a somewhat greater vertical thickness than in the smaller species of *Cervus*. The postzygapophyses are small and present outward as well as downward. As compared with the axis of *Antilocapra*, that of *Blastomeryx* is of almost the same antero-posterior length, but the surface for articulation with the atlas is wider, the median contraction less pronounced and the whole centrum more massive; the base of the spine is also thicker. But these differences are slight; in general, the axis is very much the same in the two forms.

The third and fourth cervical vertebræ are likewise of very similar construction to those of the prong-buck; the centra are of almost exactly the same length as in that animal, but the neural arches are somewhat shorter, and thus the gaps between the successive arches are larger; the arches are also distinctly wider transversely. The zygapophyses project more beyond the pedicels of the arch. The neural spines are very low, though better developed than in *Antilocapra*; on the third vertebra the spine is anteriorly a single ridge, which projects beyond the front of the neural arch and behind bifurcates into two ridges, one running to each of the postzygapophyses. On the fourth the posterior ridges are low, but the anterior rises into a distinct but very short spine. On the corresponding vertebræ of the prong-horn these ridges are indicated only in the feeblest way.

Measurements.

	B. ANTILOPINUS.	A. AMERICANA.
	M.	M.
Length of centrum of axis.....	.062	.064
Width of anterior face of axis.....	.048	.044
Third cervical, length of centrum.....	.050	.052
Fourth cervical, length of centrum.....	.054	.051

The fore limb is represented by a broken humerus, with the ulna, radius and cannon-bone nearly complete. The length of the humerus cannot be determined, as the proximal end is missing, but apparently it was about equal to that of *Antilocapra*. On the other hand, the shaft is heavier, especially in the transverse dimension, than in that animal and the deltoid ridge much more roughened and prominent and descending farther. The anconeal fossa is deep, but notably small, and the supratrochlear fossa is shallower and less distinctly marked than in the modern genus. The trochlea is wider and the intercondylar ridge even more prominent and has a more oblique course, downward and inward; the external condyle for the radius is relatively somewhat broader; the internal epicondyle is distinctly larger. The distal end of the humerus is much like that of *Dicroceros* in the less uniform vertical height of the trochlea, which tapers towards the outer side, and in the more external position of the intercondylar ridge (cf. Filhol, No. 13, Pl. XXXVIII, Fig. 4).

The ulna is somewhat more reduced than in *Palæomeryx furcatus* and less so than in the American antelope, and, so far as can be judged from the only available specimen, was not coössified with the radius at any point. The olecranon is missing, but appears to have projected more decidedly backward than in *Antilocapra*. The proximal radio-ulnar articulation is very different from that of the last-named genus, especially in its much greater vertical diameter and in the larger size of the external radial facet, which, however, is set off less distinctly from the body of the bone. The radio-cubital arcade is longer than in the prong-buck, but owing to the shape of the ulnar shaft is narrower. The shaft is very thin and compressed, but proximally has a considerable antero-posterior diameter, which diminishes rapidly as we pass downward. The distal end has but a slight fore-and-aft dimension, but is somewhat thickened transversely and is deeply notched to receive the external angle of the radius.

The radius (Pl. VI, Fig. 49) is but little shorter than that of *Antilocapra*, but has quite a different shape; the lateral and antero-posterior curvatures of the bone are very much as in the recent genus, while the shaft is much broader and less rounded, of oval transverse section and more uniform diameter, much compressed antero-posteriorly, except for the lower one-third of its length. Filhol's figure of the radius of *Palæomeryx magnus* (No. 13, Pl. XXVIII, Fig. 3) shows a very similar shaft, except for a more pronounced lateral flexure which approximates a sigmoid curvature and for a narrower proximal end. The radius of *Blastomeryx*, so far as its general shape is concerned, is more like that of the fallow deer than of the prong-buck. The trochlea is wider than in the latter, the groove for the intercondylar ridge of the humerus is narrower and emarginates the anterior border more deeply,

and the ridge external to that notch is wider in correspondence with the more mesial position of the intercondylar ridge. The process for the attachment of the external ligament is a sharp, compressed ridge, which is not so prominent as the massive tubercle of the prong-horn's radius, and hence the latter, though having a narrower trochlea, measures more across the proximal end than does that of *Blastomeryx*. The distal end differs little from that of the prong-horn, though owing to the broader shaft it expands relatively less; on the anterior face is a broad sulcus for the extensor tendons, bounded by sharp ridges, the inner one of which bifurcates near the distal face, forming a second and much narrower sulcus. The carpal facets are very modern in character, except for the less width of the lunar surface, and run very obliquely across the distal face from before backward and mesially; the scaphoid and lunar facets are separated throughout by a sharp ridge and both are reflected far up upon the posterior side of the radius. As in existing ruminants, the radius has expanded so as to come into contact with the cuneiform, though the facet for that bone is much smaller than in the prong-buck.

Nothing is known of the carpus, but it may be inferred from the facets of the radius that the lunar is relatively less expanded than in most existing Pecora.

The metacarpus (Pl. VI, Fig. 50) is in the shape of a well-defined cannon-bone, consisting of the coalesced third and fourth metacarpals; no trace of the laterals (ii and v) is preserved, but they were nevertheless probably present in very reduced form, as may be confidently inferred from the condition in *Cosoryx*. The cannon-bone is considerably shorter than that of the prong-buck, is distinctly stouter and of quite different shape. In *Antilocapra*, *Cosoryx* and *Blastomeryx gemmifer* the proximal end is much compressed in the antero-posterior direction, but in *B. antilopinus* this compression is slight, the transverse diameter but little exceeding the fore-and-aft. The latter diameter diminishes steadily towards the distal end, increasing slightly above the phalangeal trochlea; the groove on the posterior face of the shaft is deeper in its proximal portion than in the prong-horn, but is not continued so far down. As in the ruminants generally, the distal venous foramen on the anterior face is extremely small. The trochleæ for the phalanges are somewhat lower than in most existing Pecora, but the carinæ are complete, extending over the entire dorsal face of the trochleæ.

No phalanges are associated with the specimen.

Measurements.

	B. ANTILOPINUS.	A. AMERICANA.
	M.	M.
Humerus, breadth of distal end.....	.041	.033
Humerus, depth of shaft above anconeal fossa.....	.032	.017

	B. ANTILOPINUS.	A. AMERICANA.
	M.	M.
Radius, length.....	.198	.205
Radius, breadth of proximal end.....	.033	.036
Radius, breadth of distal end.....	.037	.033
Radius, breadth of middle of shaft.....	.024	.021
Cannon-bone, length.....	.181	.206
Cannon-bone, breadth of proximal end.....	.026	.027
Cannon-bone, depth of proximal end.....	.021	.019
Cannon-bone, breadth of distal end.....	.032	.026

The femur is badly mutilated, having lost the articular portions of both extremities, and yet the part which remains is longer than the entire femur of *Antilocapra*; the shaft is arched forward, compressed and deep, and is decidedly heavier and of less cylindrical shape than in the recent type. The distal portion is trihedral in section and quite massive; the supracondylar fossa is more deeply marked and rugose and the linea aspera is more prominent.

The tibia is very similar to that of the prong-horn and of almost exactly the same length, but heavier and of more massive construction throughout. The spine is lower and less distinctly bifid, the cnemial crest heavier, more prominent and descending lower upon the shaft. On the posterior face the roughened lines for muscular attachment are much more prominent and rugose. The lower portion of the shaft is less rounded, broader and more oval in section; the distal end is broad and heavy; the fibular facet is altogether distal and shows that the fibula was reduced to a mere nodule. The internal malleolus is very long, the posterior intercondylar ridge or tongue is better developed than in the prong-horn, and the sulcus for the flexor tendons is rather more deeply incised.

The tarsus (Pl. VI, Fig. 51) is completely modernized and may be briefly passed over, as it presents but few characters of interest. The astragalus is both higher and wider than in *Antilocapra* and in general outline is very similar to Fraas' figure of *Palæomeryx furcatus* (No. 16, Pl. VIII, Fig. 13). The pit for the distal median tongue of the tibia is much shallower than in the recent form and the facet for the internal malleolus less deeply incised. The articular surface for the sustentaculum is very large and passes without interruption into the distal trochlea; the latter is almost equally divided between the cuboid and navicular surfaces.

The calcaneum is remarkably long, much more so than in the prong-buck or *Palæomeryx furcatus*; this elongation, however, chiefly affects the tuber, the portion distal to the sustentaculum being of nearly equal length in all three species. The tuber is deeper (dorso-plantar diameter) and of more uniform depth than in *Antilo-*

capra, tapering less towards the free end. The sustentaculum, fibular and calcaneal facets present no noteworthy peculiarity.

As in the Pecora generally, the cuboid and navicular are coössified; the compound bone is somewhat broader and of about the same vertical height as in the prong-horn. The distal facets on the cuboid portion are quite different from those of *Palæomeryx furcatus* as figured by Fraas (No. 16, Pl. VIII, Fig. 12); the surface for the main part of mt. iv is broader, especially in front, while that for the posterior hook of the same metatarsal is very much smaller.

The length of the hind cannon-bone cannot be determined, as none of the specimens are complete. It is evident, however, that it exceeded the fore cannon-bone in this respect more than is usually the case in the prong-horn. The proximal end is of subquadrate shape, the breadth and depth of the head being nearly equal and of the same dimensions as in the specimen of *Antilocapra* which has been employed for comparison. The hind cannon-bone clearly shows that the portion which articulates with the entocuneiform is the rudiment of the second metatarsal; mt. v is probably represented also, but this is not so obvious. The proximal portion of the shaft is narrow and deep; the groove on the anterior face is strongly marked and terminates distally in a large venous foramen.

Measurements.

	B. ANTILOPINUS.	A. AMERICANA.
	M.	M.
Femur, length	(est.) .252	.223
Tibia, length256	.256
Tibia, depth of proximal end046	.041
Tibia, depth of distal end.....	.037	.033
Tibia, width of distal end.....	.034	.030
Astragalus, length.....	.039	.032
Astragalus, width of distal end.....	.024	.021
Calcaneum, length.....	.084	.075
Calcaneum, length of tuber calcis.....	.051	.045
Cubo-navicular, breadth.....	.030	.027
Cuboid, height.....	.016	.017
Hind cannon-bone, width of proximal end.....	.025	.025
Hind cannon-bone, depth of proximal end.....	.024	.024

Restoration. In general appearance and size *Blastomeryx antilopinus* must have been very like the existing American antelope. The simple, straight and erect horns constitute one striking difference between the two species, and the fossil animal had heavier limbs, lacking the extreme lightness and elegance which are so characteristic of the prong-horn. In the latter the fore and hind legs are of nearly equal length, while in *Blastomeryx* the hind limbs must have been considerably longer than the fore. The differences are, however, less obvious than the resemblances.

Camelidæ.

POEBROTHERIUM Leidy.

Proc. Acad. Nat. Sci. Phila., 1847, p. 322.

The lower beds yielded a number of more or less fragmentary remains of this genus, the teeth showing perhaps a stronger tendency to assume the prismatic form than do the earlier species from the White River and Oregon beds.

PROTOLABIS Cope.

Proc. Acad. Nat. Sci. Phila., XXVIII, p. 145.

From the upper beds were obtained several specimens of small camels which should probably be referred to this genus. Only one of these is worthy of more than passing notice. This specimen is an axis (Pl. VI, Figs. 52, 53) which is of interest as demonstrating the mode of development of the spout-shaped odontoid in the camels. I have elsewhere shown that while *Procamelus* has a spout-like odontoid quite similar to that of the existing tylopodans, the White River *Poebrotherium* has a flat or semiconical process. In the specimen before us the margins have become slightly elevated, giving the process a somewhat concave upper surface and representing the same stage as that shown by the John Day genus, *Miohippus*, among the horses. So far as the odontoid process is concerned, the horses and camels thus form exactly parallel series, though all the steps of the change did not occur contemporaneously in both lines.

PROCAMELUS Leidy.

Proc. Acad. Nat. Sci. Phila., 1858, p. 89.

This genus is represented by a number of fragmentary specimens from the upper beds, but they add nothing whatever to our knowledge of the genus.

PROBOSCIDEA.

MASTODON PROAVUS Cope.

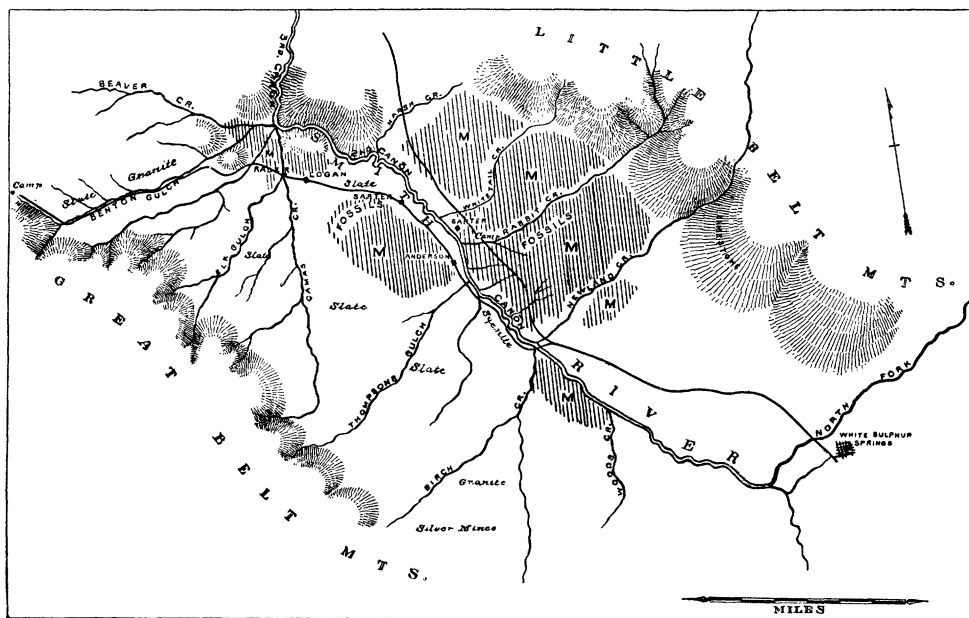
Synopsis of New Vertebrata from the Tertiary of Colorado, 1873, p. 10.

Some vertebræ and fragments of limb bones, which doubtless belong to this species, confirm Cope's statement that this is the oldest horizon containing *Mastodon* which has yet been found in America. The bones were found in position only in the uppermost beds, but loose fragments were found in the middle of the upper series. Except stratigraphically, these specimens are of no especial interest.

SUMMARY.

It will be convenient to sum up briefly here the principal results of this investigation.

(1) The beds of the Deep River valley belong to two horizons, as originally pointed out by Grinnell and Dana. These horizons differ widely in lithological character and even more markedly in their contained fossils, and are almost certainly separated by an unconformity of erosion, which represents a considerable lapse of time. The lower series should be placed at the summit of the John Day and the upper at the base of the Loup Fork, where they form a well-marked subdivision (the *Ticholeptus* beds of Cope). This subdivision is not certainly known in other regions than the present one, and the deposits in Oregon, Nebraska and Wyoming which have been referred to it most probably belong to the Loup Fork proper.



MAP OF UPPER SMITH RIVER VALLEY, MONTANA.

Drawn by W. B. Harris from a sketch by O. C. Morton.

(2) The nearest European equivalent of the upper Deep River beds appears to be the upper Miocene of Sansan and Simorre.

(3) In the genus *Cynodesmus*, which has the dentition of *Canis* combined with the skull and brain of the more ancient genera of the phylum, we find an important link in the genealogy of the dogs, leading back to the White River form, *Daphænus*, through some as yet unknown genus of the lower John Day, which, however, must have been not unlike the so-called *Temnocyon josephi*. The abundance of Miocene

dogs in North America, contrasted with their absence or unimportance in Europe, renders it very probable that the family originated in the former continent.

(4) The name *Anchitherium* has been improperly applied to American equines from the White River and John Day, and should be replaced by *Mesohippus* and *Miohippus*, the latter genus extending through the John Day and into the Loup Fork.

(5) *Desmatippus* is a new genus of equines which nearly fills the gap between *Miohippus* and *Protohippus*, the molar teeth being intermediate in character between the two, brachyodont, and yet with a thin deposit of cement in the valleys.

(6) A quite unexpected discovery is that of a species of *Anchitherium*, of the type of the European *A. aurelianense*. The genus is very probably of American origin, and, as Schlosser and Mme. Pavlov have suggested, was almost certainly not in the direct line of equine descent, but it has paralleled the true horses in many interesting ways, such as the spout-shaped odontoid, etc.

(7) Surveying the series of equine genera, which there is such good reason to believe constitute an actual line of descent, we find a steady advance in differentiation in the main, accompanied by alternating progression and regression in minor details. It is also very probably true that a slight degree of specialization in a direction away from that taken by the main line, is not incompatible with a place in that line, as is exemplified by the peculiar character of the elbow joint in *Mesohippus*, which is greatly diminished in *Miohippus* and dies out in succeeding genera.

(8) Some of the accessory tubercles in both the American and European species of *Anchitherium* appear to favor the view of "indeterminate variation."

(9) The rhinoceroses of the Old World separated at a very early period from those of the New and cannot well have any common ancestor nearer than the Acera-theria of the Oligocene; the American series has, however, run parallel to the European in many important details of structure.

(10) *Mesoreodon*, a new genus of oreodonts from the lower beds, agrees with *Eporeodon* of the John Day in most characters of skull and dentition (though with some resemblances to *Merychyrus*) while the feet are altogether like those of the latter genus. Very curious features of this genus are the presence of an ossified thyroid cartilage of the larynx, a rudiment of the bony clavicle and a metacromial process of the scapular spine. It is suggested that the large acromion of the artiodactyls, and its absence in even the Eocene perissodactyls, may be correlated with the earlier loss of the clavicle in the latter group.

(11) The skeleton of the oreodont genus, *Merycochaerus*, is now almost completely known, which permits exact comparison with other members of the group.

(12) *Merychyrus* is probably to be derived from *Oreodon* through *Eporeodon* and

Mesoreodon; its resemblances to *Merycochaerus* are due to parallelism and not to relationship. Hence it is impossible to unite these two genera, as has been proposed.

(13) *Leptauchenia* is a White River genus, and the difficulty caused by supposing the three genera of this line to be contemporaneous thus disappears.

(14) A second and somewhat smaller species of *Blastomeryx* is described from the upper beds, and considerable portions of the skeleton show that this species was in size and general appearance very similar to the prong-horn antelope, though with many cervine features. The genus is shown to be closely allied to the European *Palæomeryx* and was doubtless derived from the Old World, nothing being known in the John Day or White River beds from which it could be descended. The peculiarities of the horns and the occipital region are such as to render it doubtful whether this genus can be ancestral to any existing form. At most, it may be so related to *Antilocapra*.

(15) The axis of *Protolabis* has an odontoid process which may be described as in the incipient stage of the spout-shape and corresponding to that of *Miohippus* among the horses. The evolution of this structure proceeded by exactly similar steps in the horses and camels and is to be correlated with the increasing length of the neck and the increased angle included between the axes of the cranium and of the cervical vertebræ.

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EXPLANATION OF THE PLATES.

Plate I.

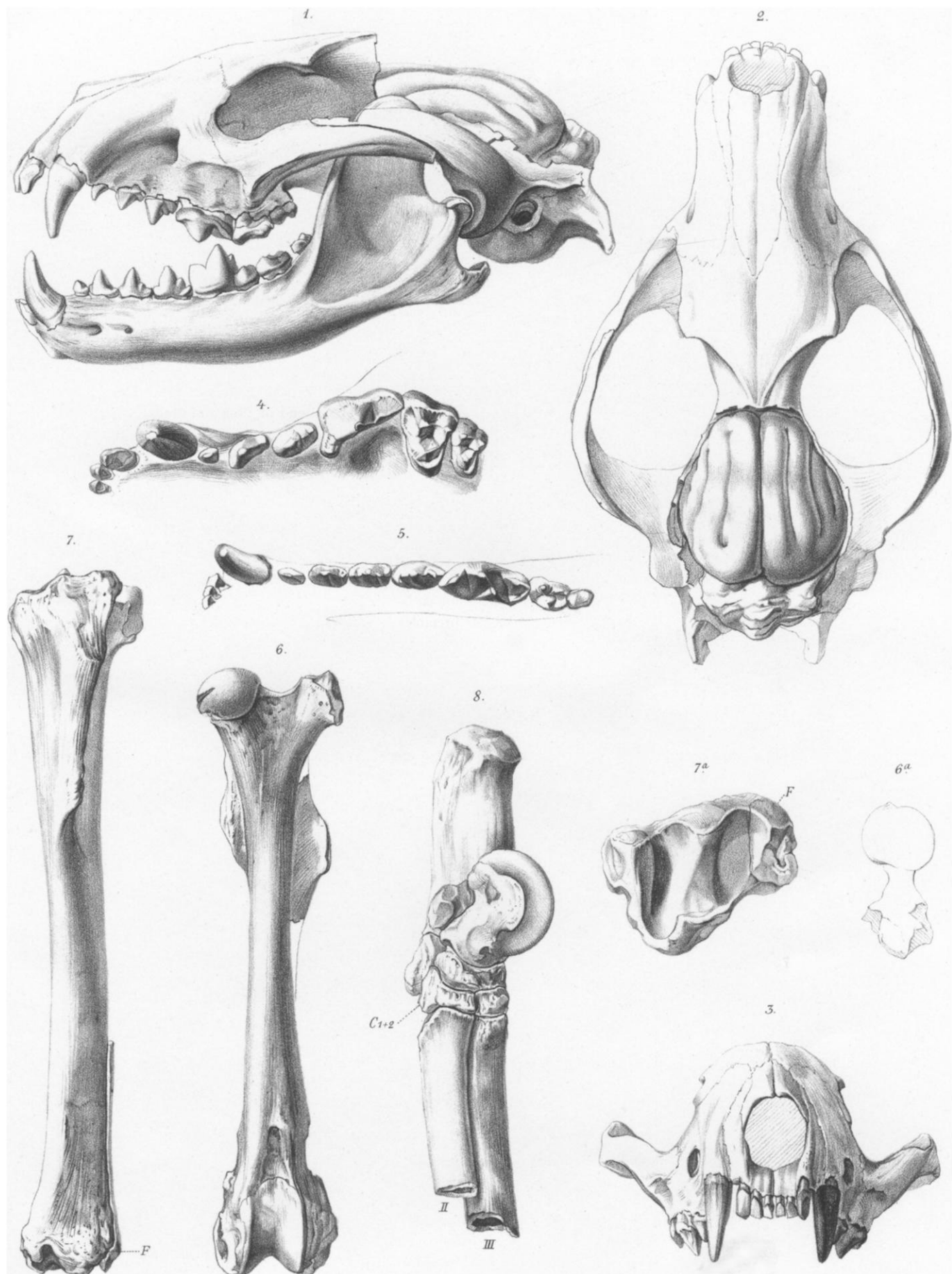
- Fig. 1. *Cynodesmus thoöides*: Skull, side view. $\times \frac{3}{4}$. Lower beds of Deep River.
 Fig. 2. " " Skull, top view. $\times \frac{3}{4}$.
 Fig. 3. " " Skull, front view. $\times \frac{3}{4}$.
 Fig. 4. " " Superior dentition, crown view, natural size.
 Fig. 5. " " Inferior dentition, crown view, natural size.
 Fig. 6. *Miohippus annectens*? Marsh: Left femur, front view. $\times \frac{1}{2}$. 6a, Proximal end of left femur.
 Fig. 7. " " Left tibia. F, fibula. 7a, Distal end of tibia and fibula, natural size.
 Fig. 8. " " Part of left pes, from inner side. $\times \frac{2}{3}$. C 1 + 2, coalesced ento- and mesocuneiforms. Lower beds of Deep River.

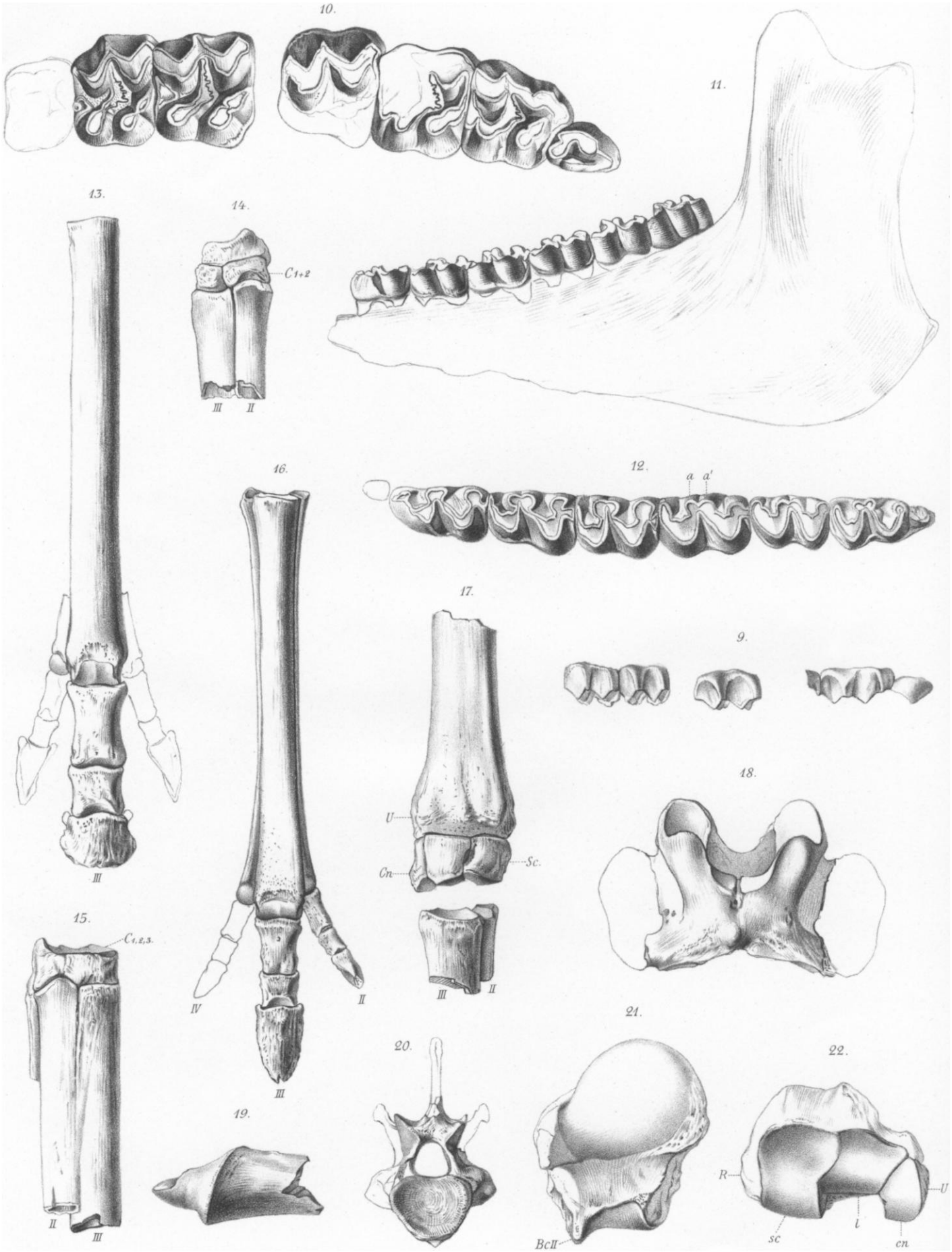
Plate II.

- Fig. 9. *Desmatippus crenidens*: Right upper molar-premolar series from the outer side. $\times \frac{2}{3}$.
 Fig. 10. " " The same, crown view, natural size.
 Fig. 11. " " Left mandibular ramus, from outer side. $\times \frac{2}{3}$.
 Fig. 12. " " Left lower molar-premolar series, crown view, natural size. a, a¹, anterior pillars of Rüttimeyer.
 Fig. 13. " " Manus. $\times \frac{1}{2}$.
 Fig. 14. " " Right pes, from inner side. $\times \frac{1}{2}$. C 1 + 2, coalesced ento- and mesocuneiforms.
 Fig. 15. *Mesohippus Bairdi* Leidy: Specimen of left pes, showing the three cuneiforms coössified (C 1 + 2 + 3); natural size. White River beds of South Dakota.
 Fig. 16. *Miohippus* sp.: Specimen of right pes, showing the very elongate and depressed ungual phalanx. $\times \frac{1}{2}$. John Day beds of Oregon.
 Fig. 17. *Protohippus* sp.: Portion of right manus. $\times \frac{2}{3}$. U, ulna; Sc, scaphoid; Cn, cuneiform. Upper beds of Deep River.
 Fig. 18. *Anchitherium equinum*: Atlas from ventral side. $\times \frac{1}{2}$. Upper beds of Deep River.
 Fig. 19. " " Fragment of axis, from the side. $\times \frac{1}{2}$.
 Fig. 20. " " Lumbar vertebra, from behind. $\times \frac{1}{2}$.
 Fig. 21. " " Proximal end of humerus. $\times \frac{1}{2}$. Bc T, bicipital tubercle.
 Fig. 22. " " Radius and ulna, distal end. $\times \frac{3}{4}$.

Plate III.

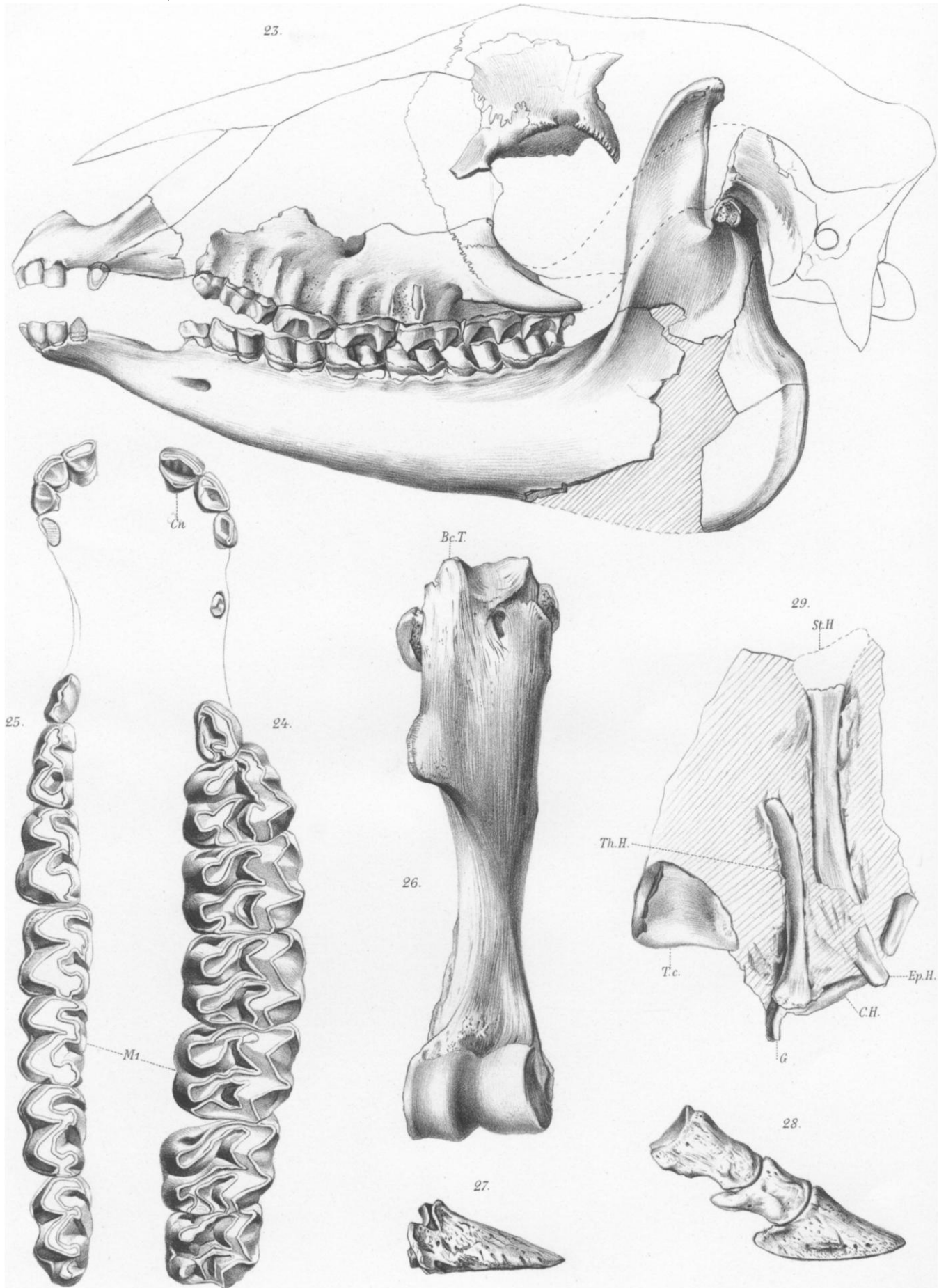
- Fig. 23. *Anchitherium equinum*: Skull, side view. $\times \frac{1}{2}$. Upper beds of Deep River.
 Fig. 24. " " Upper dentition, crown view. $\times \frac{3}{4}$. Cn, cingulum of incisor.
 Fig. 25. " " Lower dentition, crown view. $\times \frac{3}{4}$.
 Fig. 26. " " Humerus, front view. $\times \frac{1}{2}$. Bc T, bicipital tubercle.
 Fig. 27. " " Ungual phalanx of iii digit, from the side. $\times \frac{2}{3}$.
 Fig. 28. " " Phalanges of ii digit, from the side. $\times \frac{2}{3}$.
 Fig. 29. *Mesoreodon chelonys*: Hyoid apparatus, natural size. St H, stylohyal; Ep H, epihyal; C H, ceratohyal; G, glossohyal process of basihyal; Th H, thyrohyal; T C, thyroid cartilage of larynx. Lower beds of Deep River.





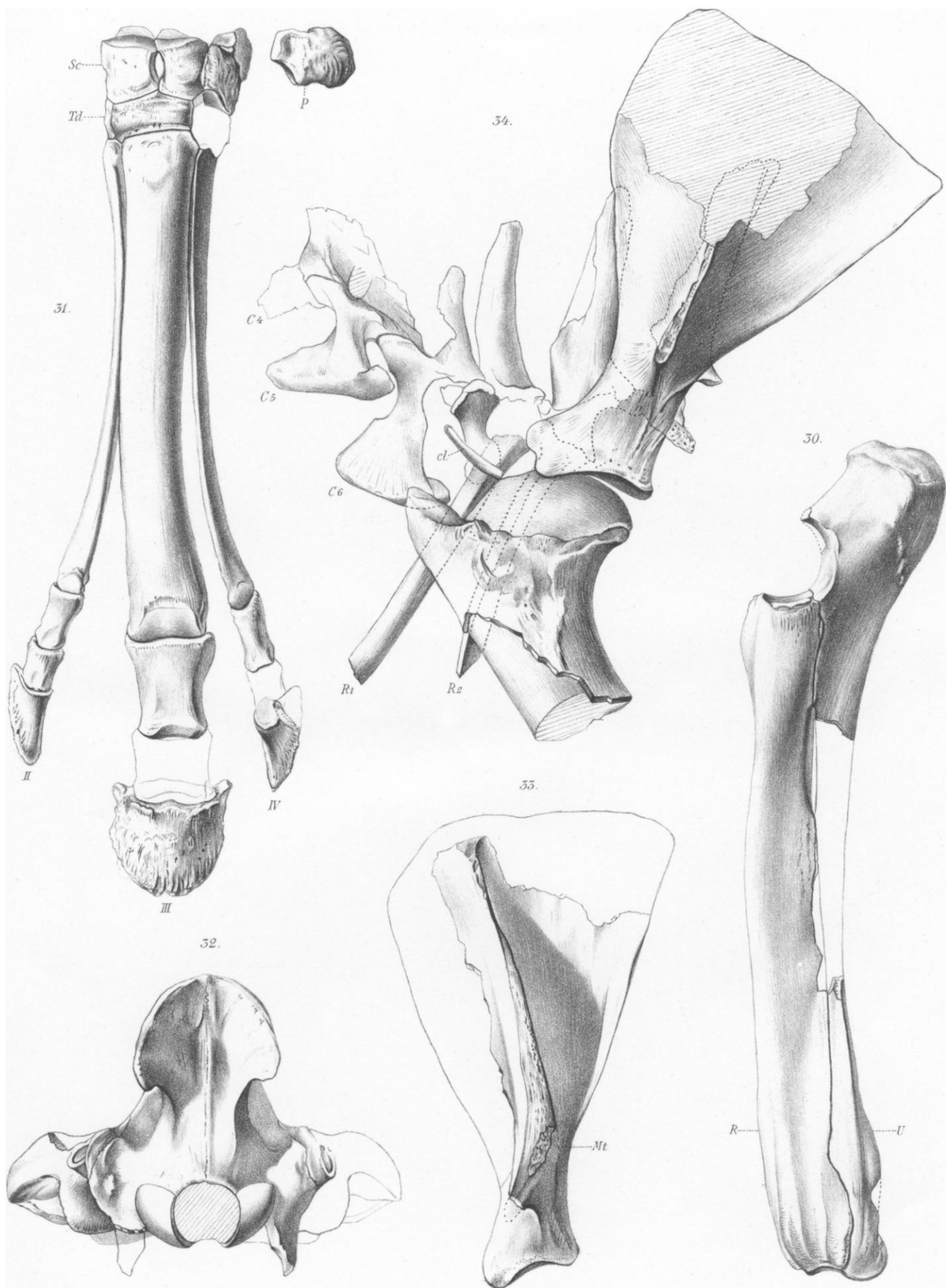
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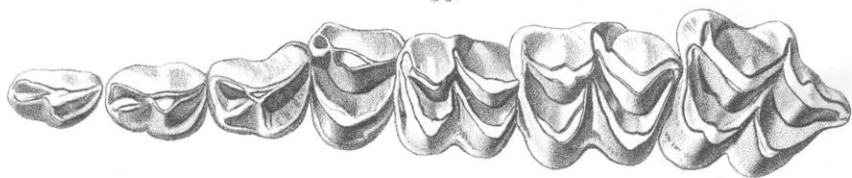


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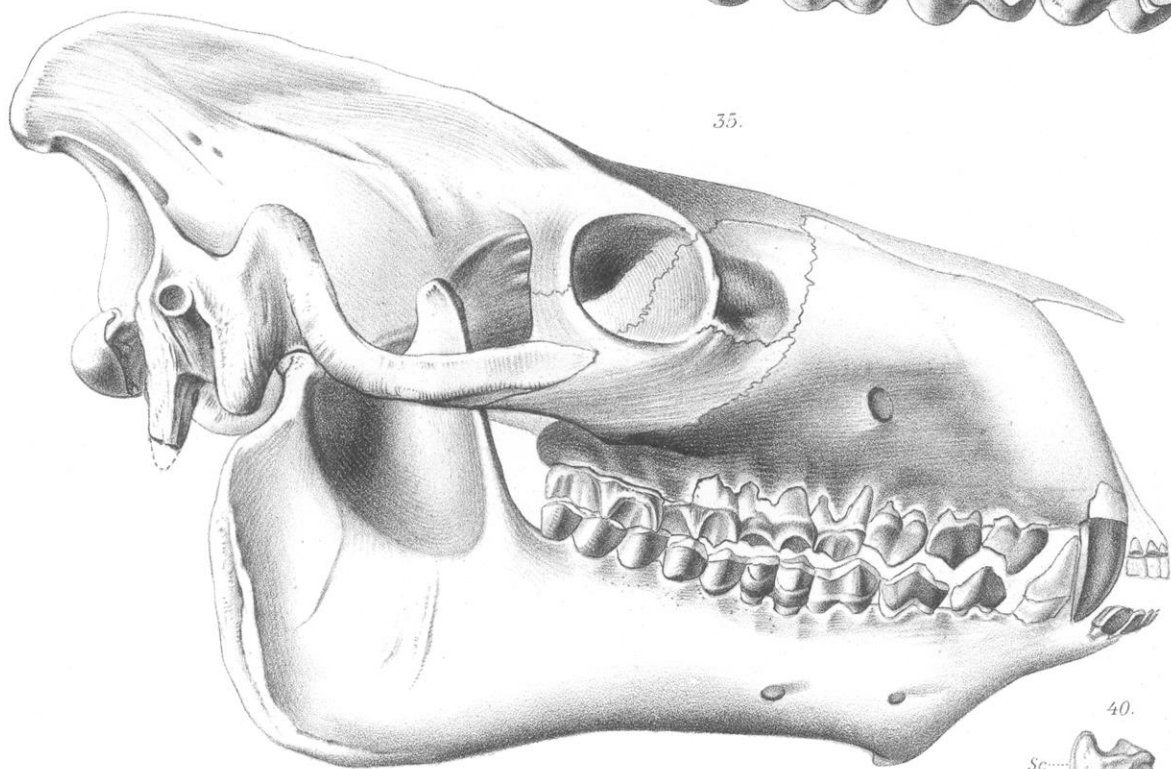
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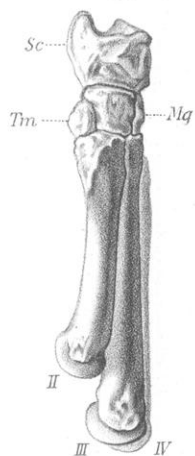
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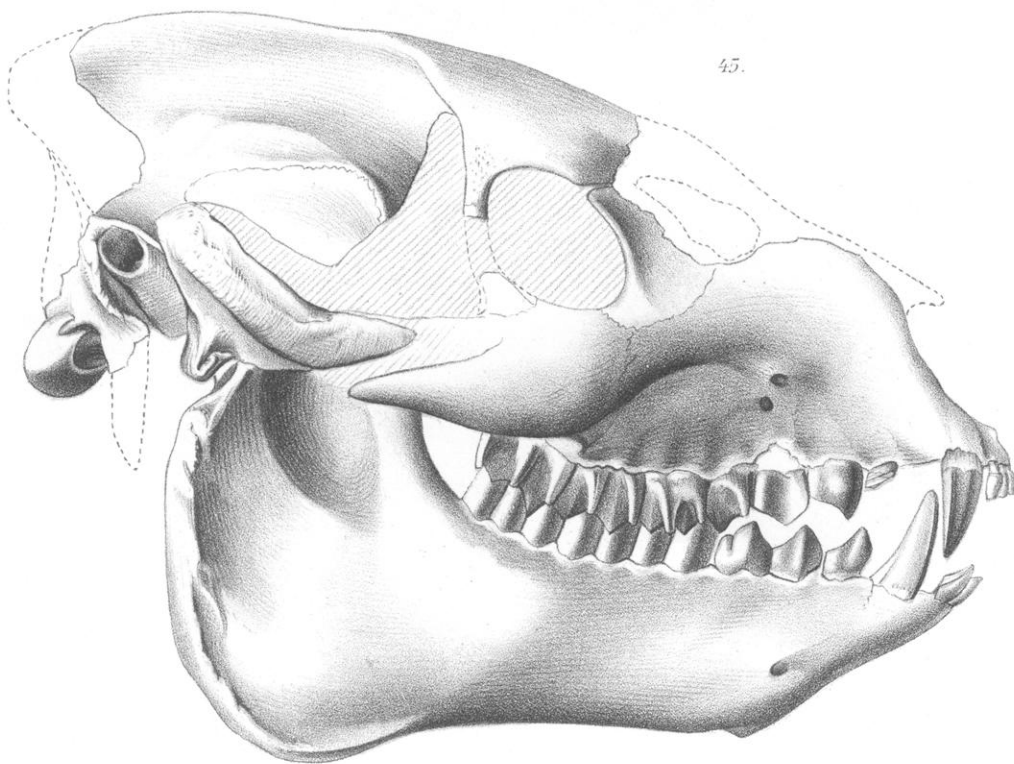
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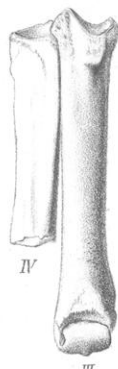
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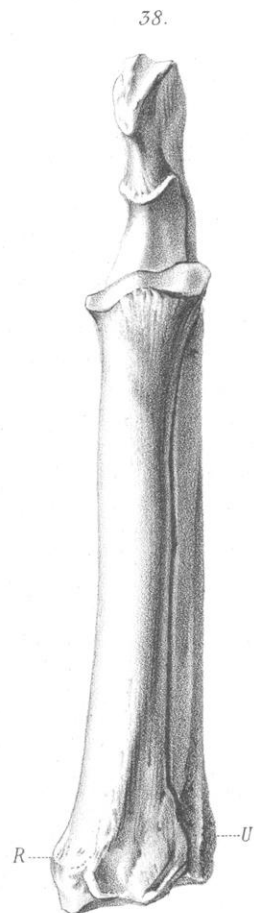
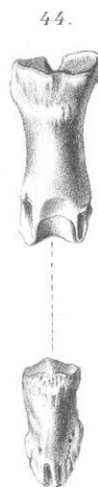
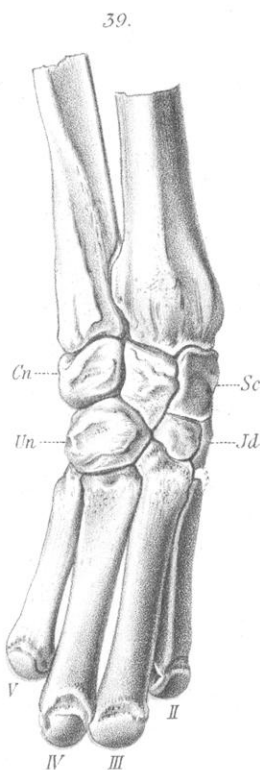
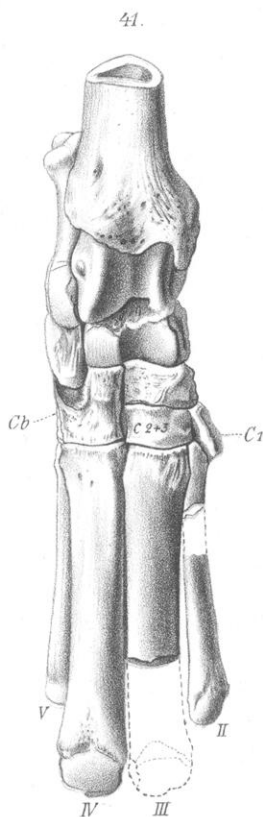
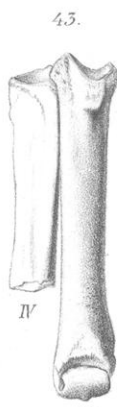
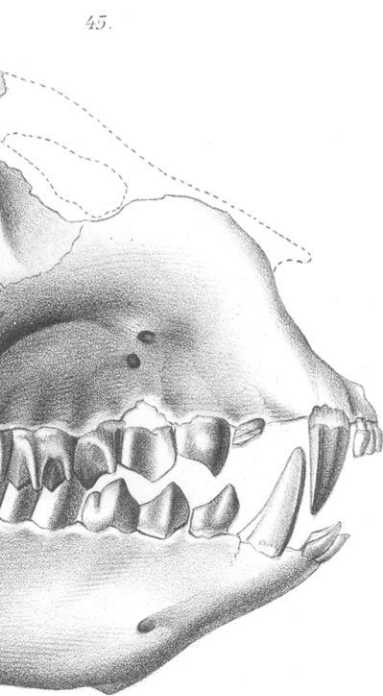
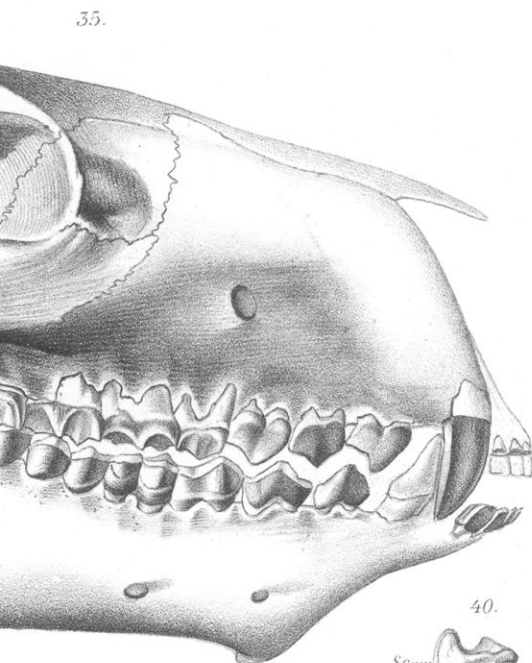
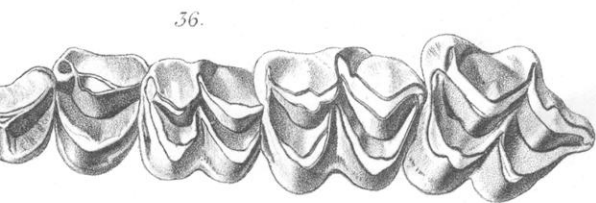


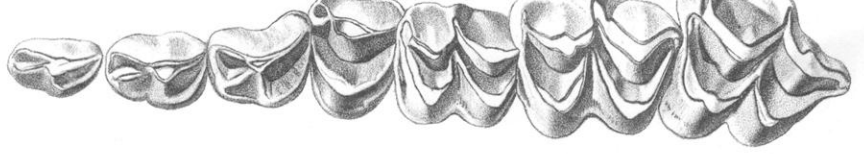
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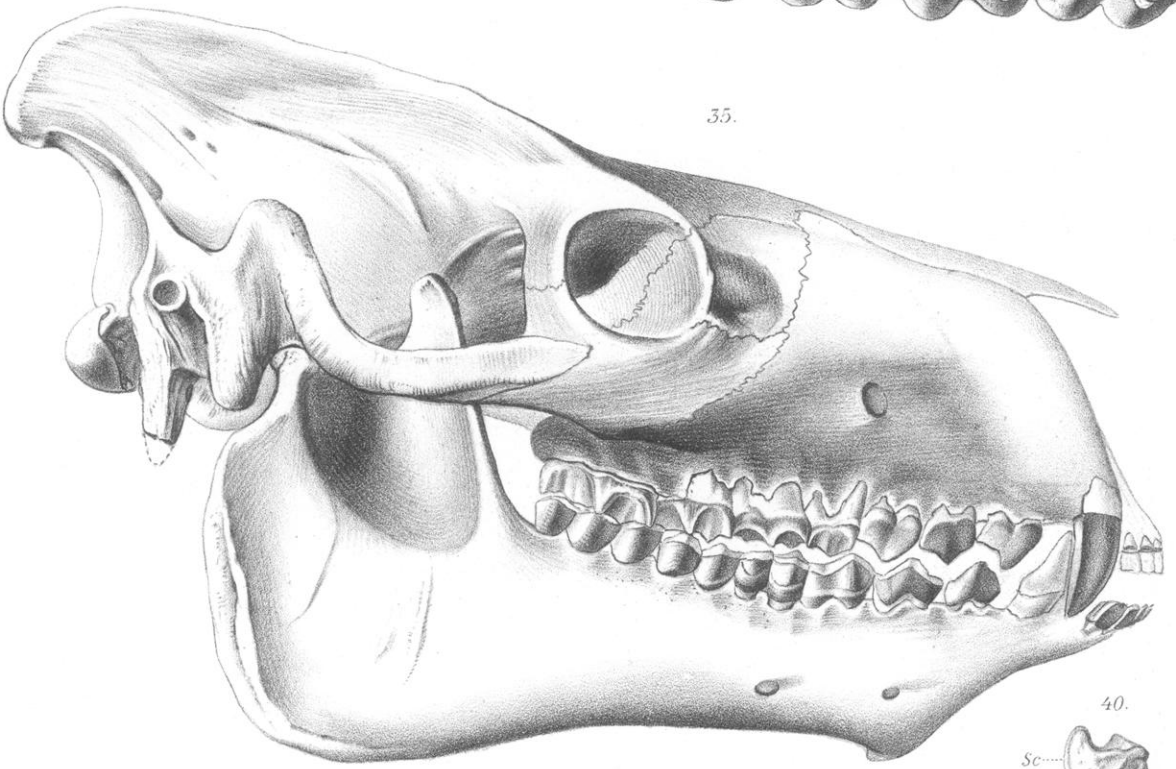
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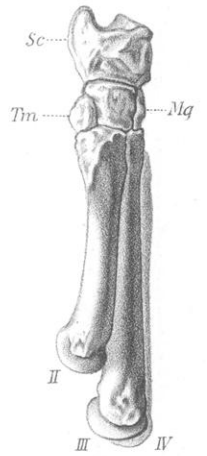




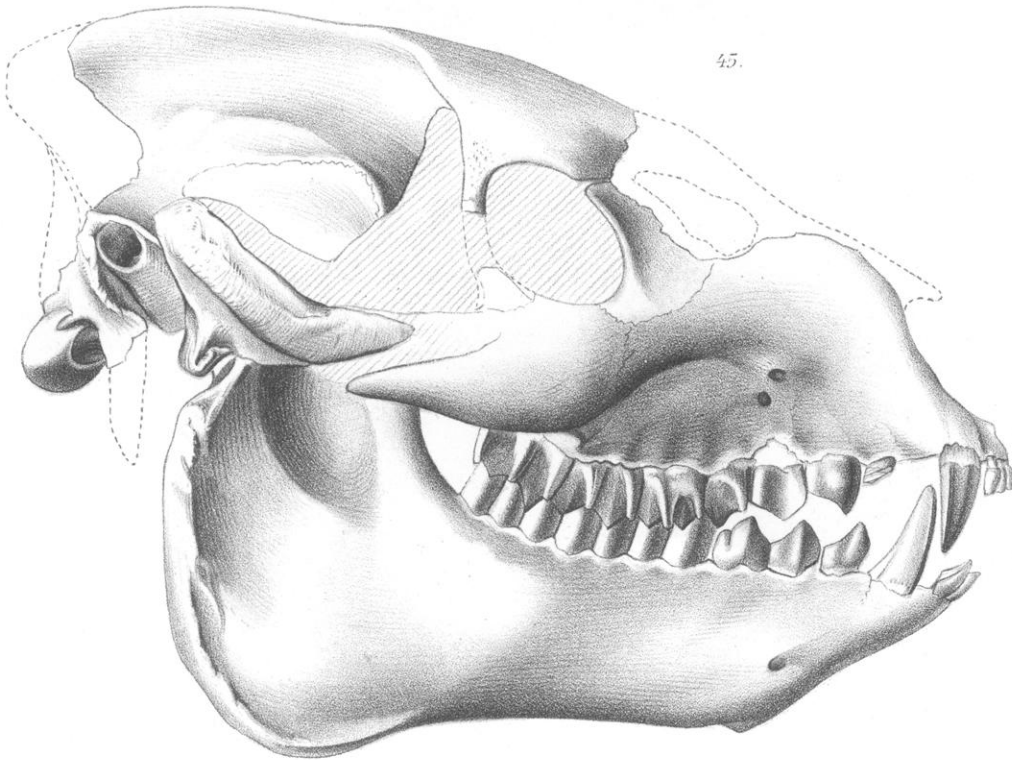
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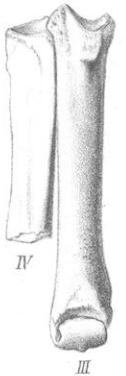
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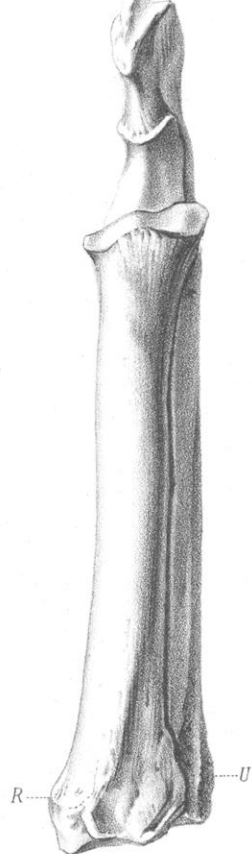
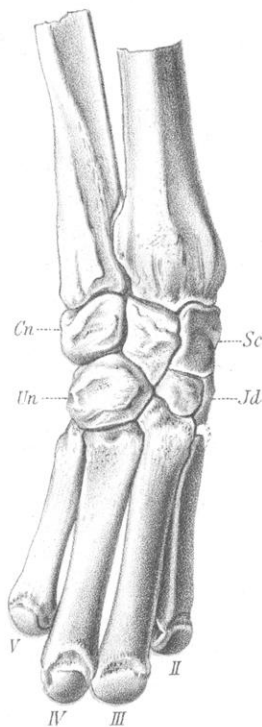
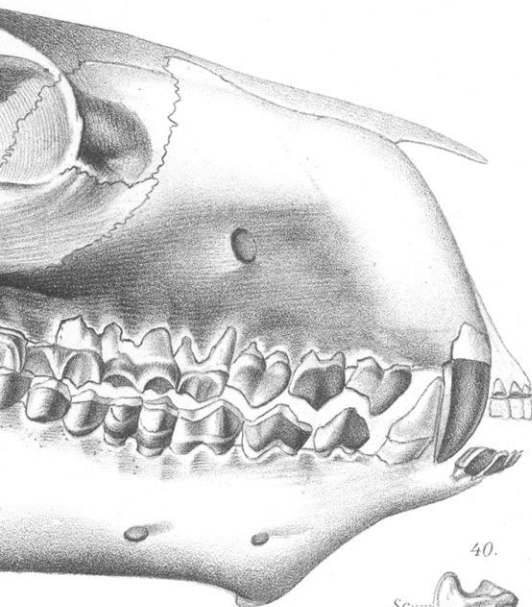
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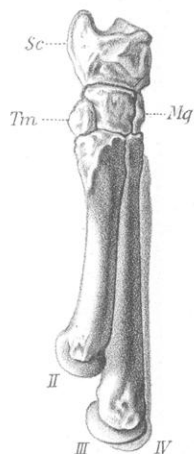
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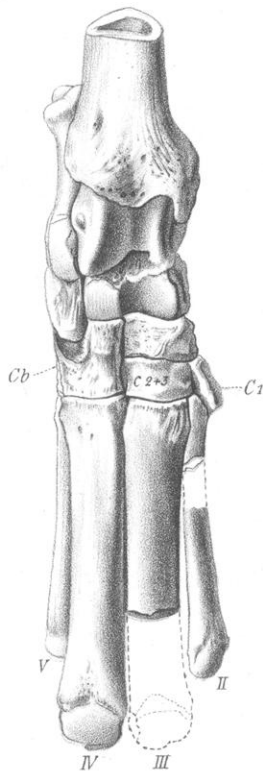
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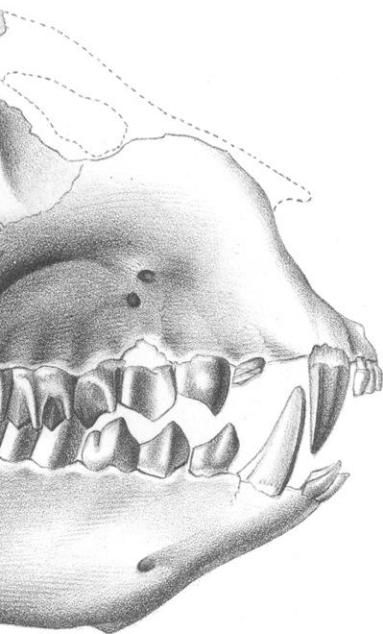
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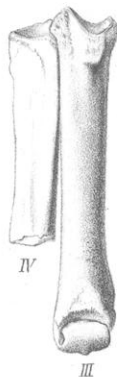
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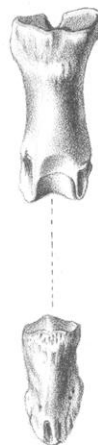
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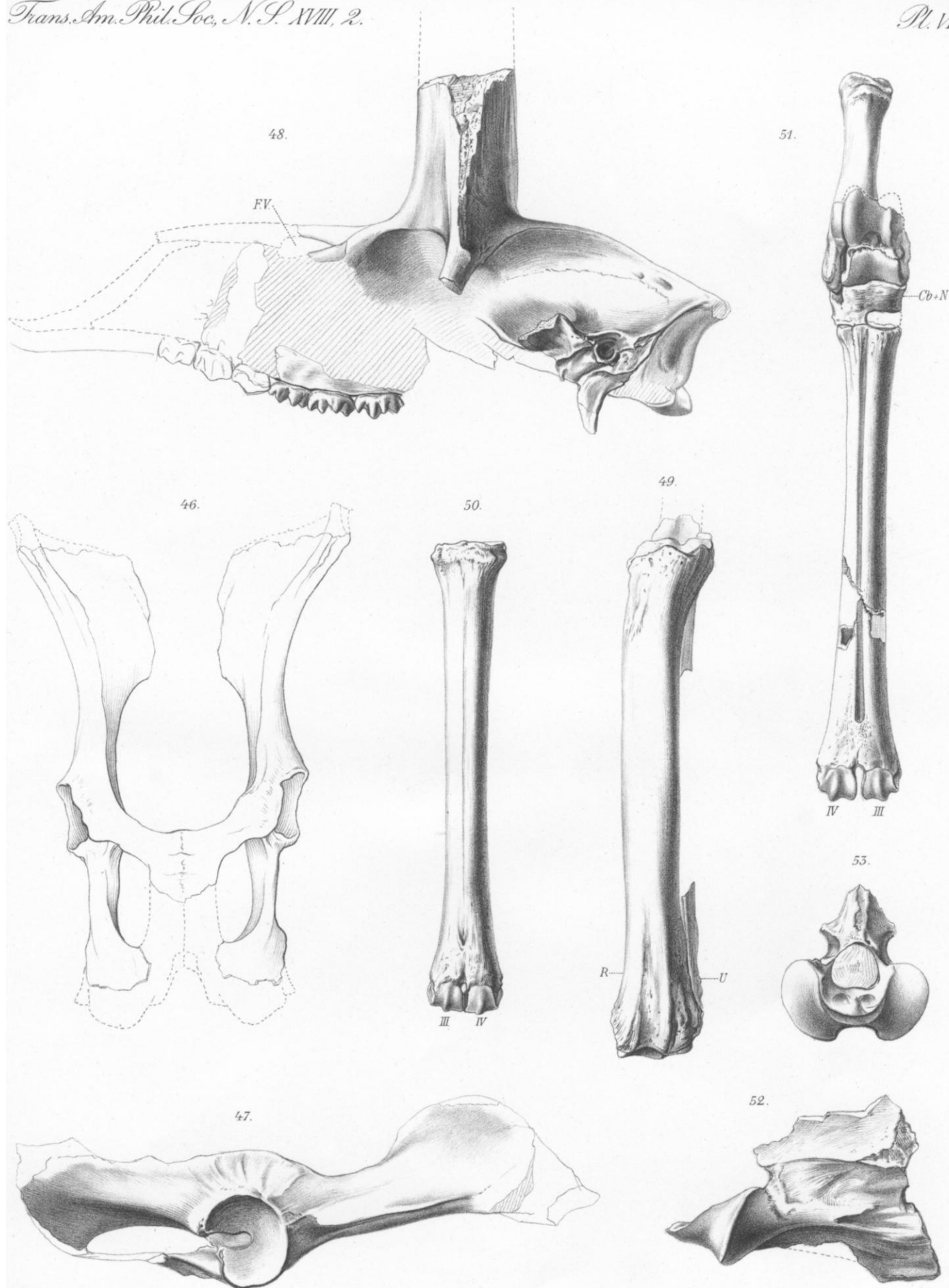


Plate IV.

Fig. 30. *Anchitherium equinum*: Radius and ulna of left side, external view. $\times \frac{1}{2}$.

Fig. 31. " " Left manus. $\times \frac{1}{2}$. *Sc*, scaphoid; *Td*, trapezoid; *P*, pisiform, from the outside.

The curvature of the metacarpals and the strong divergence of the lateral digits from the median are due to distortion.

Fig. 32. *Mesoreodon chelonys*: Skull, rear view. $\times \frac{2}{3}$. Lower beds of Deep River.

Fig. 33. " " Left scapula of supposed female. $\times \frac{2}{3}$. *Mt*, metacromion.

Fig. 34. " " Block containing cervical and thoracic vertebræ, scapula, etc., referred to same individual as male skull (Pl. V, Fig. 35). *C 4*, *C 5*, *C 6*, fourth, fifth and sixth cervical vertebræ. *R 1*, *R 2*, first and second ribs of left side; *cl*, supposed rudimentary clavicle.

Plate V.

Fig. 35. *Mesoreodon chelonys*: Skull of supposed male, side view. $\times \frac{2}{3}$. Lower beds of Deep River.

Fig. 36. " " Upper dentition of left side, crown view, natural size. Second individual.

Fig. 37. " " Left humerus, front view. $\times \frac{2}{3}$.

Fig. 38. " " Left ulna and radius. $\times \frac{2}{3}$.

Fig. 39. " " Right manus. $\times \frac{2}{3}$.

Fig. 40. " " Left manus, from inner side. $\times \frac{2}{3}$. *Tm*, trapezium.

Fig. 41. " " Right pes. $\times \frac{2}{3}$.

Fig. 42. " " Phalanges of third digit of pes, natural size.

Fig. 43. *Mesoreodon intermedius*: *Mc. iii* and *mc. iv* of right manus. $\times \frac{2}{3}$. Lower beds of Deep River.

Fig. 44. " " Phalanges of *iii* digit of pes, natural size. Second individual.

Fig. 45. *Merychys zygomaticus* Cope: Skull of type specimen, from the side. $\times \frac{2}{3}$. Cope collection. The double infraorbital foramen is conjectural. Upper beds of Deep River.

Plate VI.

Fig. 46. *Mesoreodon chelonys*: Pelvis, from ventral side. $\times \frac{2}{3}$.

Fig. 47. " " Left os innominatum. $\times \frac{2}{3}$.

Fig. 48. *Blastomeryx antilopinus*: Skull, from left side. $\times \frac{1}{2}$. Upper beds of Deep River. *F V*, facial vacuity, or fontanelle.

Fig. 49. " " Left radius and ulna, from the front. $\times \frac{1}{2}$.

Fig. 50. " " Cannon-bone of left manus. $\times \frac{1}{2}$.

Fig. 51. " " Right pes. $\times \frac{1}{2}$. *Cb + N*, coalesced cuboid and navicular. The cannon-bone is from a second individual.

Fig. 52. *Protolabis* sp.: Axis, from the side. $\times \frac{2}{3}$. Upper beds of Deep River.

Fig. 53. " " The same, front view. $\times \frac{2}{3}$.